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A

TREATISE ON ZOOLOGY

EDITED BY

E. RAY LANKESTER

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PART V

MOLLUSCA

BY

PAUL PELSENEER, D.Sc.

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PREFACE

THE manuscript of Dr. Pelseneer's volume on the Mollusca—now published—was completed nearly two years ago. It has been translated and revised for press by Dr. Gilbert Bourne, of New College, Oxford, to whom the thanks of both the author and editor are due and are cordially tendered.

E. RAY LANKESTER.

December 1905.

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CHAPTER I

THE MOLLUSCA

PHYLUM MOLLUSCA, Cuvier

(= Palliata, Latreille; Malacozoa, de Blainville; Heterogangliata, Owen; Otocardia, Haeckel: Saccata, Hyatt).

Grade A. Isopleura (Ray Lankester).
  Class I. Amphineura (von Jhering).
    Order 1. **Polyplacophora.**
    ,, 2. **Aplacophora.**

Grade B. Prorhipidoglossomorpha (Grobben).
  Class I. Gastropoda (Cuvier).
    Sub-Class 1. Streptoneura.
      Order 1. **Aspidobranchia.**
      ,, 2. **Pectinibranchia.**
    Sub-Class 2. Euthyneura.
      Order 1. **Opisthobranchia.**
      ,, 2. **Pulmonata.**
  Class II. Scaphopoda (Bronn).
    (No Orders.)
  Class III. Lamellibranchia (de Blainville).
    Order 1. **Protobranchia.**
    ,, 2. **Filibranchia.**
    ,, 3. **Eulamellibranchia.**
    ,, 4. **Septibranchia.**

Grade C. Siphonopoda (Ray Lankester).
  Class I. Cephalopoda (Cuvier).
    Sub-Class 1. Tetrabranchia.
    ,, 2. Dibranchia.
      Order 1. **Decapoda.**
      ,, 2. **Octopoda.**

I. INTRODUCTION.

FORMERLY a number of very diverse zoological forms, such as Brachiopoda, Tunicata, and even Cirrhipedia, were included among the Mollusca. The last-named were the first to be dissociated from the true Mollusca, after J. Vaughan Thompson had shown, by a study of their larval development and metamorphoses, that they were modified Crustacea. At a later date the Tunicates were shown, also as a result of embryological research, to have affinities with the Vertebrata. The Brachiopoda, both because of their bivalve shell and the supposed resemblance of their superficial anatomy to that of Lamellibranchia, retained a place in the Molluscan phylum for a much longer period. H. Milne-Edwards, it is true, united the Brachiopoda with the Polyzoa under the name Molluscoidea, but he placed this group very close to the Mollusca, and his views were very generally accepted by zoologists. It is only twenty-five years since the phylum Mollusca was finally purged of all alien elements, and limited, as in Professor Lankester's "Mollusca" in the ninth edition of the *Encyclopædia Britannica*, 1883, to such forms as are demonstrably related to one another.

More recently H. von Jhering propounded the view that this assemblage of animals, believed to be closely related to one another, was in fact unnatural, heterogeneous, and polyphyletic. But his hypothesis could not stand the test of criticism, and never obtained the support of any reputable malacologist. Since his time the unity of the Molluscan phylum has never been called into question.

Closely related as the different forms of the Mollusca are, they exhibit a great variety in external aspect, chiefly because the tegumentary layer, consisting of epithelium, connective tissue, and muscle, is exceedingly plastic, and gives rise to outgrowths, appendages and expansions of the most various kind. The diversity of form is further increased by concrescence of the various out-growths of the body, either with one another, or with adjacent structures; such concrescences being exhibited by the mantle edges, the lobes and margins of the foot, the gills, and other organs.

But, however diverse the external configuration of the Molluscan body, the internal organisation, at least in its main features and in young forms, preserves a remarkable uniformity. The group is homogeneous, sharply defined, and its members are easily recognised. The Mollusca also afford a very good instance of the progressive modification and evolution of organic structure. It would be difficult to name another group of the animal kingdom in which relationships can be more clearly determined and the pedigrees of the sub-groups more certainly traced; and for this reason no phylum, with the possible exception of the Echinoderma, has, in recent years, yielded such fruitful results to the investigator.

II. THE MORPHOLOGY AND LIFE-HISTORY OF THE MOLLUSCA.

1. *General Description and External Characters.*—The Mollusca are Coelomocoela with a distinct coelom and haemocoel. The latter has undergone a great development by phlebœdesis (see Professor Lankester's introduction in Part II. of this treatise), and the coelom therefore is proportionately reduced. In the adult condition there are two recognisable coelomic cavities, the pericardial coelom and the true gonocoel or gonadial cavity. These two may be in communication with one another, but more frequently they are separate. The haemocoel is completely closed, and is probably the remnant of the embryonic blastocoel. The coelom, on the contrary, communicates with the exterior by coelomoducts and coelomopores. The coelomoducts are part of the primitive protocoelom; they first served as gonaducts, but afterwards were adapted to excretory functions and became excretory organs or uroducts. In some cases, however, they retain part of their primitive character and serve the double purpose of uroducts and gonaducts (Fig. 5^{bis}, *g*, *i*, *j*).

The external features of a mollusc, though very variable, nearly always admit of a division of the body into three tegumentary regions or organs. The most anterior division is the head: it bears the mouth, appendages of various kinds, and nearly all the organs of special sense. The second division is ventral, and has the form of a highly developed tegumentary projection of variable shape: this is the foot, the chief organ of locomotion. The third division comprises the dorsal part of the body, covered by a calcified cuticle or protective shell, the shape of which is subject to great variation in the different subdivisions of the phylum. This dorsal region is known as the mantle or pallium.

The free surface of the body is covered by an epithelium, which is frequently ciliated. The epithelium is richly supplied with glandular cells which secrete an abundant mucus, serving to keep the skin moist and supple. In some cases, *e.g.* *Phyllirhoë* and *Pholas*, the glandular secretion is phosphorescent. The epithelium is also richly supplied with nerve-endings, and some of the epithelial cells may secrete chitinous or calcareous spicules, which remain embedded in the integument (Amphineura).

The greater part of the external, or at least the originally external, pallial epithelium secretes a shell (Fig. 1, *sh*). The shell consists of a matrix of a chitin-like substance, conchyolin, impregnated with mineral salts. The latter may be present in such abundance as to form 95 per cent of the shell substance. The chief mineral constituent is carbonate of lime, but from 1 to 2 per cent of phosphate of lime is also present, and traces (less than $\frac{1}{2}$ per cent) of carbonate of magnesium. The greater part of the thickness of the shell is made up by the ostracum, which consists of two layers: (1) an external layer, frequently coloured, and formed by prisms of calcite; (2) an internal layer consisting of arragonite, generally in the form of overlapping plates: it is the internal layer that forms, in various species, the nacre or mother-of-pearl.

The growth of the shell is effected in two ways. Its extent is increased by the addition of new matter, secreted by the thickened edge of the mantle, to the outer or prismatic layer. Its thickness is increased by addition of new matter, secreted by the whole surface of the mantle, to the inner or nacreous layer. In addition to the two layers of the ostracum already mentioned, there is a third layer, called the hypostracum, on the areas of attachment of the muscles which serve to fasten the animal to its shell. Finally, there is the periostracum or shell epidermis, forming an external covering to most shells: it is formed by the pallial fold at the edge of the mantle. In some Polyplacophora, Gastropoda, and Lamellibranchia, and in most of the Cephalopoda, the free edges of the mantle are reflected over the shell, so as to cover a greater or less part of its outer surface. In some species in which this special feature is developed to its greatest extent, the reflected mantle edges form a completely closed sac round the shell, so that the latter is internal and concealed. In rare cases the pedal integument may secrete a calcified "shell," which may be adherent (*Hipponyx*) or free (*Argonauta*).

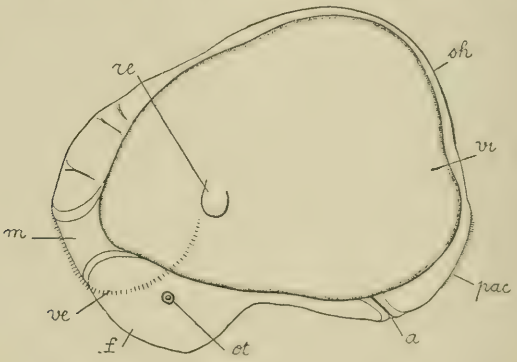

Fig. 1.

Young embryo of *Purpura lapillus*, from the left side, × 16. *a*, anus; *f*, foot; *m*, mouth; *ot*, otocyst; *p.a.c*, post-anal cilia; *re*, embryonic kidney; *sh*, shell; *ve*, velum; *vi*, vitellus.

The shell was for a long time the criterium of Molluscan classification. But the progress of anatomical study showed that genera with more or less similar shells might differ considerably from one another in internal organisation, and gradually the structure of the animal, rather than the form of its shell, came to be recognised as the guide to its systematic position. But to this day there are many genera of Gastropods and Lamellibranchia whose anatomy is unknown, and their classification, founded on the characters of their shells alone, is, of course, provisional.

The head and foot are fastened to the shell by muscular bundles, which are paired and symmetrical in the Polyplacophora, Scaphopoda (Fig. 181, *c′*), and Lamellibranchia (retractors of the foot), and in the Cephalopoda (retractors of the head and funnel), but in the Gastropoda there is a single asymmetrical so-called "columellar" muscle (Fig. 45, *co*). The fibres of these muscles are attached to the epithelium under the shell. The connective tissue layer which lies beneath the tegumentary epithelium is mesodermic in origin, and is extensively developed in the Mollusca. It invades the greater part of the original blastocoel and presents the following varieties: (1) plasmatic or vesicular cells, which sometimes give rise to endoplastic calcareous concretions or even to true sub-epithelial spicules, as in *Pleurobranchus* and various Nudibranchia; (2) stellate cells; (3) fibrillar cells. Blood spaces, whose distension causes turgescence of various parts of the body, are frequently found in this connective tissue. On the other hand, the connective tissue may become compact and form supporting structures; such are the "skeleton" of the gill filaments, the sub-epithelial "shell" of the Cymbuliidae, and the cartilaginous pieces in the Cephalopods and in the buccal mass of all classes except Lamellibranchs.

Below, or imbedded in the subcutaneous connective tissue, are muscle fibres forming layers of rectilinear or annular bundles; but as a rule only a few definite muscular masses can be distinguished. The muscle fibres are of the smooth variety, though in certain cases they appear to be striated, especially in muscles which contract rapidly. Such apparently striated fibres are found in the buccal mass of various Gastropods, in the heart, in the fins of Pteropods and Heteropods, in the siphon of Cephalopods, in the columellar muscle of the larvae of certain Nudibranchs, in the branchial septum (*Cuspidaria*), in the adductor muscles of various Lamellibranchs, and especially in the Pectinidae, in which the striation looks almost identical with that of Arthropods and Vertebrates. These fibres, however, are usually regarded as unstriated: they are wholly bi-refringent. The fibrillae are parallel to one another, but in the contracted state are thrown into spirals, which is said to produce the appearance of transverse striation. The subject calls for renewed investigation.

The tegumentary layer, composed as described of epithelium, connective tissue, and muscles, may attain to a very considerable thickness. Certain portions of the tegumentary organs can be spontaneously detached from the body by the reaction of the animal against the incidence of external forces. This phenomenon is known as "autotomy," and is generally defensive, as, for instance, the loss of portions of the foot (*Harpa*) or of its appendages; the loss of the siphons of some Lamellibranchs; of the dorsal papillae and other parts of the dorsal integument in certain Nudibranchs; of the cephalic tentacles of Scaphopods, etc. The lost parts are regenerated, just as other tegumentary organs (cephalic tentacles, fins, arms of Cephalopods) that have been accidentally removed, are regenerated with all the complex and differentiated structures that they may possess, such as eyes, suckers, etc. The most remarkable example of regular physiological autotomy is found among the Cephalopods, namely, the hectocotylised arms of the Philonexidae and Argonautidae (Fig. 287).

2. *The Digestive Tract.*—The alimentary tract always has two orifices, the mouth and anus, generally situated at the two extremities of the body; but the anus may be brought to an anterior position by a ventral flexure, which may or may not be complicated by a lateral torsion. The anus is absent only in the parasitic genus *Entosiphon*; the alimentary tract is rudimentary in the parasites *Entocolax* and *Entoconcha*; it is absent altogether in *Enteroxenos.*

In all other forms three essential parts can be recognised in the digestive apparatus. Firstly, the buccal or anterior section of the gut, of ectodermic origin, which comprises the first dilatation or buccal cavity and the oesophagus. Secondly, there is the mid-gut, of endodermic origin, comprising the second dilatation or stomach. Thirdly, there is the hind-gut or intestine. The anterior dilatation or buccal cavity is absent in the Lamellibranchs, with the exception of certain Nuculidae. Cuticular formations are present in different parts of the internal wall of the alimentary tract, and are specially developed in its anterior portion. They occur around the mouth—having the form of a prehensile collar in *Doris*—but more particularly in the buccal cavity, where two different sorts of cuticular formations are found, the mandibles and the radula. The mandibles are anterior, dorsal, and unpaired in the Dentaliidae, Patellidae, Pulmonates, *Aegirus* (Fig. 73, B), etc., but paired and lateral in the majority of the Gastropoda. In the Cephalopoda the members of the pair are dorsal and ventral (Fig. 266). These organs are chitinous, and are only calcified in certain Chaetodermidae, and partially so in *Nautilus.*

The radula is characteristic of the phylum Mollusca. It exists throughout the series, from the most archaic forms upward, and is only absent in the most specialised types, in which it has evidently been lost, such as certain Neomeniomorpha among the Aplacophora, the Lamellibranchs, various isolated forms of Gastropoda, and the Cirrhoteuthidae among Cephalopods. The radular apparatus has the form of chitinous teeth, disposed in transverse rows; the number of teeth in each row is subject to variation, but they are always arranged symmetrically on one side and the other of a central tooth (Fig. 2).

Thus there are eight lateral teeth on either side of the central tooth in Polyplacophora (8.1.8); two laterals on either side of the central in Scaphopoda (2.1.2); three laterals on either side of the central in almost all Cephalopods (3.1.3). In the Gastropods the number of teeth in each row varies considerably in the different sub-groups. The radular ribbon issues from a pharyngeal caecum, in which it is secreted, and is applied to the surface of paired cartilaginous pieces situated on the floor of the buccal cavity. These so-called cartilages have a characteristic vesicular structure quite different from that of ordinary cartilage such as is found in Cephalopods and Opisthobranchs. Applied to these cartilaginous pieces the radula, by the action of special muscles, executes backward and forward rasping movements.

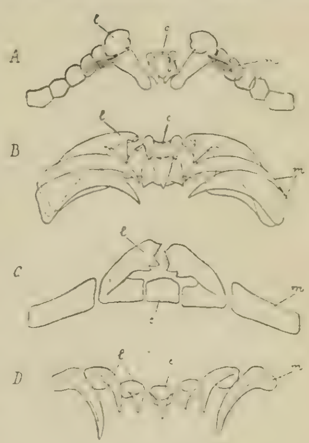

Fig. 2.

Transverse rows of the radula. *A*, *Boreochiton ruber*; *B*, *Natica clausa*; *C*, *Pulsellum tetragonum*; *D*, *Rossia glaucopis*; all much enlarged. *c*, central tooth; *l*, lateral teeth; *m*, marginal teeth. (After G. O. Sars.)

The cuticular lining of the stomach is specially developed in Lamellibranchs and in certain Gastropods in which it is sometimes differentiated into masticatory plates provided with special muscles.

The buccal cavity or anterior dilatation of the alimentary tube receives in the Amphineura, Gastropoda, and Cephalopoda, the secretion of the so-called salivary glands, of which one or several pairs may be present. The oesophagus may present various forms of accessory dilatations, known as "gizzards," glandular regions, etc.

The secretion of an important and voluminous digestive gland is poured into the second primary dilatation of the gut or stomach: this gland is called the liver, but this name must not be taken to imply a physiological identity with the liver of vertebrates. The liver is an acinous glandular organ, the epithelial cells of which are all very similar to one another in Polyplacophora, but in other forms they are generally differentiated into ferment cells and excretory cells. From the physiological point of view this gland is a hepato-pancreas, since its secretion peptonises albuminoids, converts starches into sugar, and saponifies fats. Absorption of digested food-stuffs is effected, in some forms at least, by the liver itself, and finally this gland has an excretory function in that it secretes waste products of metabolism into the alimentary tube.

The stomach (in various Gastropods, in Scaphopods, and Lamellibranchs) is provided with a caecum in which a crystalline style is often secreted. In addition there exists, in some Gastropods and Cephalopods, a caecum coiled in a spiral. These two structures do not appear to be homologous, for in some Gastropods (*Nassopsis*) the spiral caecum and the sac containing the crystalline style occur together. The intestine, or at least its terminal portion, is furnished, in nearly all groups of Mollusca, with a longitudinal ridge called a typhlosole or with a furrow bordered by two ridges. An anal gland is present in various Gastropods, in *Dentalium*, and in nearly all Cephalopods.

3. *Circulation and Respiration.*—In addition to the cavity of the alimentary tube two other important cavities, completely separated from one another, are found in the Molluscan body. The first, called the coelomic cavity, communicates freely with the exterior, and is generally reduced to the pericardium and the gonadial or genital cavity. The second is very probably the remnant of the blastocoel or segmentation cavity, and is continuous with spaces in the conjunctive mesenchyme of the integuments. It is filled with a fluid blood or haemolymph which is at once nutritive and respiratory in function. This cavity constitutes the circulatory apparatus.

The circulatory apparatus is provided, for a greater or less part of its extent, with proper endothelial walls; where these are absent it is lined by connective tissue so that the organs are never brought into direct contact with the blood. The circulatory cavity is, in fact, more or less specialised into arteries and veins of vascular structure, but there are rarely tubular capillary ramifications, except in the integuments of Cephalopods. More usually the capillaries are swollen irregular cavities. The rest of the circulatory system is formed of *sinuses*;—irregularly defined spaces in the connective tissue and specially abundant in the integuments. In fact, the phenomenon of phleboedesis (Ray Lankester) is manifested in a very high degree in the Mollusca, the cavity of the circulatory system being distended and insinuated among the organs to such a degree as to push back and diminish the coelom, though no communication is ever established between the two. The blood-vessels pass abruptly into the sinuses, and in some cases communication between sinus and blood-vessel is established by orifices in the walls of the latter. Remarkable instances of this form of communication may be seen in the vena cava of *Nautilus*, in the auricle of *Patella* (Fig. 80), and in the afferent branchial vein of *Aplysia*.

The central and pulsatile portion of the circulatory apparatus is well developed, except in the Entoconchidae. It is situated on the dorsal side in the pericardium, except in *Anomia* and the Octopods, and originally at the posterior end of the animal. In no case is the pericardium a blood sinus; it is a portion of the coelom, without communication with the circulatory system, as is shown by the absence of red corpuscles in the pericardium of such Molluscs as have red blood (Penrose and Ray Lankester).

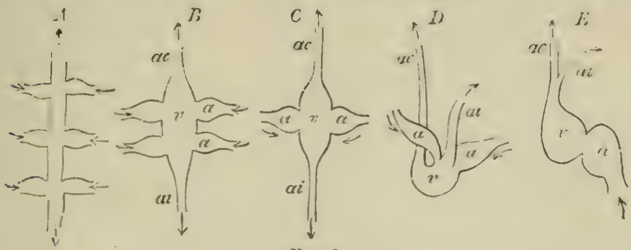

FIG. 3.

Diagram to show the relations of the heart in the Mollusca. *A*, part of the dorsal vascular trunk and transverse trunks of a Chaetopod worm; *B*, ventricle and auricles of *Nautilus*; *C*, of a Lamellibranch, of *Chiton*, or of *Loligo*; *D*, of *Octopus*; *E*, of a Gastropod. *a*, auricle; *a.c*, arteria cephalica (aorta); *ai*, arteria abdominalis; *v*, ventricle. The arrows show the direction of the blood-current. (From Lankester, after Gegenbaur.)

The heart is entirely arterial, and comprises, firstly, a median ventricle, with muscular walls and internal fleshy columns, the fibres of which give the appearance of striation: being spongy in texture, this organ has no intrinsic nutritive vessels. Secondly, two (in *Nautilus* four) paired auricles, disposed symmetrically on either side of the ventricle. The auriculo-ventricular openings are simple, except in the Polyplacophora, where they are frequently multiple (Fig. 4). Each opening is provided with a valve opening towards the cavity of the ventricle and preventing the reflux of blood into the auricle. Frequently one member of the single pair of auricles is much reduced, or may be aborted, as is the case in the majority of Gastropods (Fig. 3, E).

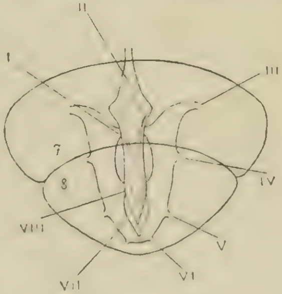

FIG. 4.

Heart of *Chiton pellis-serpentis*, dorsal aspect. I, left anterior auriculo-ventricular communication; II, ventricle; III, right anterior afferent vessel; IV, V, VI, right posterior afferent vessels; VII, left auricle; VIII, left posterior auriculo-ventricular communication.

Primitively a single, morphologically anterior aorta is given off from the ventricle, and this condition persists in the Amphineura and in the archaic Lamellibranchia.

The aorta together with the ventricle forms a dorsal vessel comparable to that of Annelids. Secondarily a second and morphologically posterior aorta may be formed, as in the Gastropods and the majority of Lamellibranchs (Fig. 3, E), and even a third (the genital aorta of certain Cephalopods) may be formed in connection with the first. The ramifications of these aortae carry the blood throughout the body. The kidneys, however, are supplied almost entirely with venous blood, from which their cells extract and excrete the waste products of metabolism. Thus the circulation of the kidneys may be described as a portal system.

The blood is generally a colourless fluid containing amoebocytes and sometimes haematids. It may be of a bluish colour, due to the presence of haemocyanin, an albuminoid containing copper (Fredericq). In other cases it is red, owing to the presence of haemoglobin, which may be in solution in the plasma (*Planorbis*) or may be localised in haematids (red blood corpuscles). These are present in *Pectunculus*, *Arca*, *Ceratisolen* [Lankester], *Poromya*, and Neomeniomorpha. The musculature of the buccal bulb has been shown by Lankester in Gastropoda to owe its red colour to haemoglobin impregnating the muscular tissue. The density of the blood is always greater than that of water, greater even than that of sea-water in the case of some marine molluscs. The blood of *Anodonta* contains ten times more salts than the surrounding medium: the density of the blood of *Octopus* is 1,047. The pressure of the blood in the arteries amounts to from 3 to 5 centimetres of water in *Anodonta* and to 108 centimetres of water in *Octopus*.

The volume of blood in some groups, particularly in the Lamellibranchs and Gastropods, is so great that it plays a very important part in the turgescence of various parts of the integument, by filling the tegumentary sinuses during the relaxation of their muscles. To this end some blood spaces, corresponding to different turgescible organs, are separated by valves which admit of the accumulation of a considerable volume of blood in a definite portion of the body. Examples of this are found in Gastropods and in the valve of Keber in Lamellibranchs.

Respiration.—The venous blood is oxygenated almost exclusively in the superficial tegumentary sinuses of the mantle, this organ receiving a comparatively feeble supply of arterial blood. A portion of the free or ventral surface of the mantle is specialised to form a respiratory organ, through which passes nearly the whole of the blood that is returned to the auricles. These tegumentary organs, enclosing a part of the vascular system, project into the surrounding water in the form of pallial expansions, normally paired, in which the blood is oxygenated. This special part of the circulatory system is often regarded as a separate organ under the name of the "respiratory apparatus." It is constituted by the ctenidia or branchiae properly so-called, of which there may be one or many pairs. There are two pairs in *Nautilus*; from four to eighty pairs in the Polyplacophora, and where a single pair is normally present it may be reduced to a single azygos organ, generally in correlation with the reduction of the auricles.

The ctenidia are situated primitively in the posterior or anal region of the mantle, but they may be multiplied and spread anteriorly, or both anteriorly and posteriorly (Polyplacophora, Fig. 28), or without being multiplied they may extend progressively towards the region opposite to their primitive situation, as in Gastropods and Lamellibranchs. They are shorter in *Nucula* than in *Arca*; shorter in *Arca* (Fig. 188) than in *Avicula* (Fig. 236); shorter in *Pleurotomaria* than in *Trochus*, and in *Trochus* than in *Fissurella*.

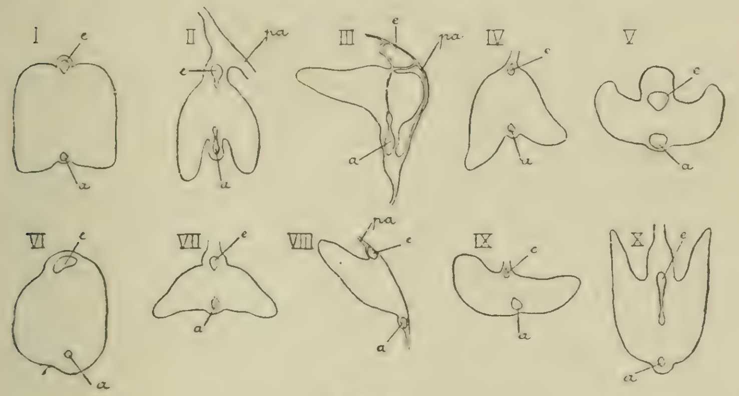

Fig. 5.

Diagrams of transverse sections of the ctenidia of various Mollusca. I, *Chiton*; II, *Pleurotomaria*; III, *Trochus*; IV, *Nucula*; V, *Nautilus*; VI, *Chaetoderma*; VII, *Haliotis*; VIII, *Lacuna*; IX, *Solenomya*; X, *Sepia*. *a*, afferent vessel; *e*, efferent vessel; *pa*, mantle.

These ctenidia have exactly the same structure in the archaic members of the different groups: an identical fundamental structure may be recognised in the Polyplacophora, in the Rhipidoglossa among Gastropods, in the Protobranchs among Lamellibranchs, and in the Cephalopods (Fig. 5). Each ctenidium consists of an axis containing two vascular trunks. The one, an afferent vessel, in which the blood current is centrifugal, communicates with a "vena cava" or with a simple venous sinus; the other is the efferent vessel, in which the current is centripetal, and the auricle is nothing more than its specialised terminal portion. The auricle, in fact, has the innervation of a pallial organ like the ctenidium; the ventricle that of a visceral organ properly so called. Each side of the axis bears a row of respiratory filaments, generally flattened, but of variable shape, whose cavities communicate with the two vascular trunks of the axis. It is in the cavities of these filaments that the blood absorbs oxygen dissolved in the water. The continuous renewal of water on the surface of the ctenidium is provided for by a covering of ciliated epithelium. The ciliated epithelium is absent in Cephalopods, but in this group the powerful musculature of the mantle and siphon is sufficient for the purpose.

The whole volume of venous blood, however, is not in all cases passed through the ctenidia: a smaller or larger part may be distributed to the mantle and thence returned directly to the heart. This arrangement is found in a considerable number of Gastropods (Heteropods, Pleurobranchs, and Nudibranchs) and in the majority of Lamellibranchs. Finally, the typical respiratory apparatus may be complicated by specialisation or by reduction, and may disappear altogether, as in the Neomemiidae, the Scaphopoda, the Septibranchia, and a large number of Gastropoda. In such cases the function of oxygenating the blood is wholly transferred to the free surfaces of the pallial integuments, which often form a secondary respiratory organ, especially in the Gastropoda. In aquatic species this secondary apparatus takes the form of "pallial branchiae," in terrestrial species of a "lung."

In certain cases there is a localised blood-gland or lymphatic gland which, from its phagocytic function and the formation of amoebocytes, may be said to have the physiological character of the spleen of Vertebrates. This organ is generally situated on the course of the aorta, instances being found in many Opisthobranchs and in the "white body" of Cephalopods (Fig. 268). It consists of conjunctive tissue in which blood corpuscles are formed at the expense of the conjunctive cells. In other cases the gland is diffuse, that is to say, distributed in a more or less irregular fashion in the conjunctive tissue in the form of plasmatic cells.

4. *Coelom.*—The walls of the coelom of Molluscs are completely covered by a continuous epithelium, partly genital, partly excretory. The coelom is divided into several different cavities, gonadial, pericardial, and renal, the two last named being excretory. The gonadial and reno-pericardial cavities are separate, except in the Cephalopods and aplacophorous Amphineura. It must be assumed that the "Prorhipidoglossa," the common ancestors of the Gastropods, Scaphopods, and Lamellibranchs, had also this communication between the pericardium and genital cavity, and it is preserved in the more archaic Gastropods and Lamellibranchs (certain Rhipidoglossa and Protobranchs), in which the gonads

open, not into the pericardium, but in the reno-pericardial duct, uniting the pericardium to the kidney. Such an arrangement is found in *Trochus*, *Solenomya*, etc. (Fig. 5^{bis}, *g*, *i*) ; and here we find that the genital and pericardial cavities are united to the kidney by a common duct of double origin, genital and pericardial. As a further differentiation, we find in a fairly large number of Lamellibranchs and in the Scaphopods that the two distinct branches of this duct become longer (Fig. 5^{bis}, *j*) ; then the common duct disappears, and the gonad opens directly into the renal sac (Fig. 5^{bis}, *h*, *k*).

The pericardial coelom always surrounds the heart except in the Octopoda and the Anomiidae, or is much reduced or absent. Sometimes prolongations, ramifications, or parts of this pericardial cavity have their walls much specialised to form an excretory apparatus, known as the pericardial glands. The pericardial coelom always communicates with the renal sacs or renal portion of the original coelom: in *Nautilus* alone the kidneys are no longer continuous with the pericardial cavity, and this latter opens directly to the exterior by "coelomopores," orifices peculiar to itself.

The Cephalopods have a pair of coelomoducts leading directly from the genital cavity to the exterior. In the Aplacophora this genital space only communicates with the exterior through the intermedium of the pericardium and renal sacs. The polyplacophorous Amphineura have acquired two special genital canals, through which the sexual products are discharged, but they do not appear to be true primitive coelomoducts (Fig. 5^{bis}, *e* ; Fig. 30, D). Finally, in the Lamellibranchs in general and in the Gastropods the genital ducts are formed at the expense of a portion of the renal sacs and ducts (on one side only in Gastropods) ; but the male ducts of the hermaphrodite Lamellibranchs, the Anatinacea, are neomorphs and an exception to the general rule.

5. *Excretory Organs.*—The essential organs of excretion are the renal sacs or urocoeles, whose morphological nature requires further elucidation. They consist of paired canals, more or less modified, which open to the exterior on the surface of the body and internally into the pericardium, except in the case of *Nautilus*, in which, as described above, the pericardial coelom has its own separate orifices, and in *Dentalium*. The reno-pericardial apertures are more or less elongate ciliated funnels whose cilia create a current in the direction of the kidney. In *Elysia* alone does the kidney possess multiple reno-pericardial apertures, to the number of about ten (Fig. 92). True "nephridia" (Lankester) only occur in the young stages of certain Gastropods (Pulmonates (Fig. 118), *Paludina*, etc.) and in Lamellibranchs ; they are described below under the head of Embryology (p. 136).

In cases in which a single pair of renal sacs is present, one member of the pair is often rudimentary or absent. This condition is found in the majority of Gastropods, where the ctenidium

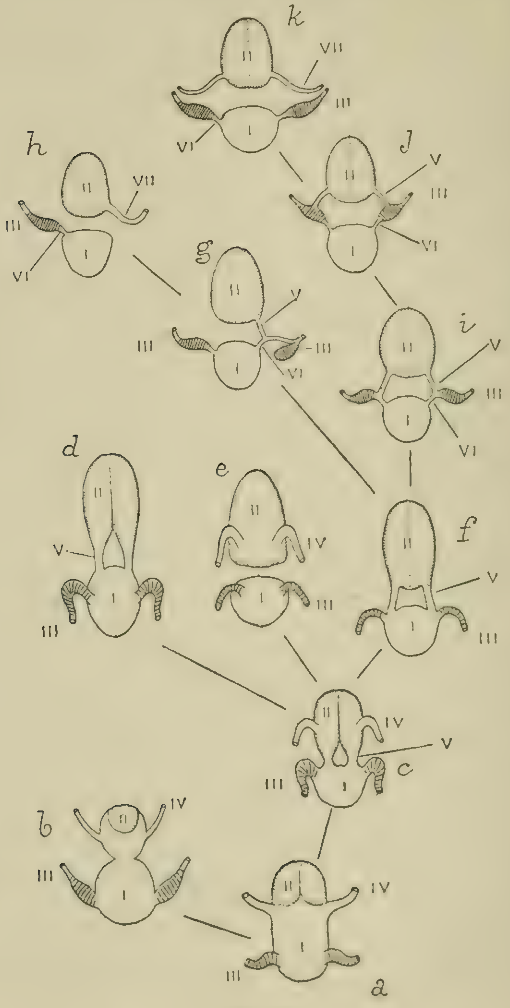
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FIG. 5bis.

Transformations of the genital duct in the Mollusca: diagrammatic dorsal views of the pericardium, gonad, and kidneys. *a*, ancestral hypothetical form; *b*, Cephalopod; *c*, stock form of Amphineura; *d*, Aplacophora; *e*, Polyplacophora; *f*, Prorhipidoglossum; *g*, some Rhipidoglossa (*Emarginula*, etc.); *h*, specialised Gastropod; *i*, Protobranch Lamellibranch; *j*, *Pecten*; *k*, Eulamellibranch. I, pericardial part of coelom; II, gonad; III, kidney; IV, genital duct of Cephalopoda and Polyplacophora; V, duct leading from the gonad into the pericardium, into the reno-pericardial duct, or into the kidney; VI, reno-pericardial duct; VII, secondary genital duct in specialised Gastropoda and Lamellibranchs.

and auricle of the same side (topographically the right side) are also atrophied or have disappeared (Fig. 55).

Almost all the venous blood that passes to the ctenidia traverses the kidneys, so that there is a renal portal system. The renal sacs are, in fact, irrigated by conduits which lead to the afferent branchial veins, and these conduits may traverse the kidneys, as in Cephalopods (Fig. 273), or may surround them, as in Septibranchs (Fig. 210). Consequently the blood passing through the ctenidia is devoid of the products of excretion.

The surface of the excretory sac which forms the kidney may be greatly increased by folds, by the formation of caeca, etc. Its walls are glandular for a greater or less part of their extent, and consist of an excretory epithelium in the cells of which the nitrogenous products of metabolism are accumulated. These products are ejected in the solid or liquid form, and vary from one group to another as regards their chemical constitution. They consist essentially of guanin in the Cephalopods, of uric acid in Gastropods, except in *Cyclostoma*, where they consist of urea, as is also the case in Lamellibranchs, in which group uric acid is not normally found. The external water does not penetrate into the kidney, nor, *a fortiori*, does it enter the pericardium. It has, however, been established that water may occasionally enter the kidney of certain Heteropods and of *Styliger*, an Opisthobranch of the family Hermaeidae.

The glandular part of the kidney is not the only region in which a glandular epithelium may be present. The epithelial lining of the pericardium may, in various groups, be specialised to form a pericardial gland (Grobben) whose excretion is more acid than that of the kidney properly so called. Such a gland may be seen on the surfaces of the auricles or in the ramifications of the pericardium in Gastropods, Lamellibranchs (Fig. 212), and in Cephalopods (Fig. 273). This glandular region has a blood supply analogous to that of the kidney, and one may even see, in *Nautilus*, the renal epithelium and that of the pericardial gland developed at the same level on the same afferent branchial vessel, the one on the one side, the other on the other side. The pericardial gland eliminates the waste products which are excreted by the Malpighian glomeruli of the vertebrate kidney; the molluscan kidney, properly so called, deals, on the other hand, with the same products of excretion as the tubuli contorti. Certain liver cells also constitute an important organ of excretion, especially in the Opisthobranchs and Pulmonates. In the latter the dorsal wall of the pedal gland is also excretory, and finally veritable accumulatory excretory organs are often formed in the conjunctive tissue by plasmatic cells known as the "cells of Leydig." True nephridia exist in developmental stages in the form of "larval kidneys."

6. *Nervous System and Organs of Sense.*—In the nervous system of Mollusca a perioesophageal collar is normally present, of which the dorsal moiety is the *cerebral* and the ventral moiety the *labial commissure.* From either side, at the junction of the two moieties of the collar, nerve cords distributed to the integuments take their origin. These latter are differentiated into a dorsal pair, innervating the mantle, and a ventral pair, innervating the foot: they may be ganglionated throughout the whole of their extent, as in the pallial cords of Amphineura and the pedal cords of Amphineura and Aspidobranchs, or they may bear localised ganglia, known as the pleural and pedal ganglia respectively, near their origins. These two paired cords are connected by anastomoses, the most anterior anastomosis being always preserved and known as the pleuro-pedal connective. The pedal cords or centres are united by anastomoses ventrad of the digestive tract, the most anterior and at the same time the largest of the anastomoses being always retained as the pedal commissure. The pallial cords are often united by an anastomosis dorsad of the rectum as in Amphineura, Cephalopods, Lamellibranchs, and various Gastropods. The nervous system of Molluscs is thus characterised by its oesophageal ring, from which issue four, originally parallel, tegumentary nervous cords (Fig. 19).

The visceral organs are innervated firstly by trunks given off from the labial commissure. These trunks, uniting under the oesophagus, form an anterior or stomato-gastric visceral commissure, bearing on its course two ganglia which are situated near and partially innervate the buccal bulb and also the whole of the oesophagus and stomach. In some cases, *e.g.* the Cephalopods and certain Tectibranchia, the stomato-gastric commissure bears stomachal ganglia. The viscera are innervated, in the second place, by trunks issuing from the pallial cords and distributed to the circulatory, excretory, and genital viscera. In all Molluscs except the Amphineura the two most important of these trunks are united below the digestive tube, thus forming an infra-intestinal loop or "visceral commissure," provided with one or more ganglionic centres (Fig. 19, *v.g*). These two visceral loops, the stomato-gastric and the visceral properly so called, are generally united together by anastomoses (Cephalopods and Gastropods).

There are, therefore, three kinds of nerve-centres in Molluscs: (1) sensory centres, represented by the ganglionated cerebral commissure or differentiated cerebral ganglia; (2) tegumentary centres, represented by the pleural and pedal cords or ganglia; (3) the visceral centres, represented by the stomato-gastric and the visceral loop properly so called.

The nerve-centres consist of a superficial portion, made up of ganglion cells, and a central fibrillar portion which is almost exclusively composed of prolongations of sensory or centripetal nerve fibres. The prolongations of the superficial ganglion cells are continued into motor or centrifugal nerve fibres. Isolated ganglion cells are to be found in the muscles of the heart and in those of the buccal bulb (Pulmonata).

The nervous system, being in close relation to all the other organs, is of great importance to the morphologist, and the more so because it is the last to be influenced by the modifications undergone by the organism. At the same time, every modification of an organ is faithfully reflected by the nervous system. In such forms as are still slightly differentiated, the large nerve cords are uniformly covered with ganglion cells: in less primitive forms the special development of certain parts of the body has produced a preponderant development of certain nerves corresponding to them, and nerve cells accumulate and give rise to ganglia at the bases of these more highly developed nerves. Accessory ganglia may also be formed at different points of the nervous system, either at the bases of sensory organs (Figs. 94, *br.g*; 214, *os*, etc.) or at the origin of important nerve trunks (Fig. 159, *i*). The ganglion centres may be shifted along the cords on which they are situated in consequence of changes in the parts that they innervate. Similarly, a nerve may be shifted along the cord from which it issues until it seems to have changed its place of origin, but its fibres always maintain their connection with their primitive nerve-centre.

The approximation or the union of two parts of the body involves the approximation or fusion of the corresponding ganglia: or if one of the two parts is atrophied, its nerve-centre is reduced and may be fused with the adjacent nerve-centre. The various ganglia exhibit a general tendency to centralisation, all the principal sensory organs being aggregated at the anterior part of the body. At first all the sensory and motor nerve-centres, and finally all the others (Cephalopoda, Nudibranchia, many Pulmonata), become localised in the same region and are grouped together.

Organs of Sense.—The function of general sensibility is spread over the whole of the free surface of the envelope of the body and the surfaces in continuity with it: included among the latter are the internal surface of the mantle, and especially its glandular tracts, and all invaginations of the ectoderm, such as the pedal glands, the terminal portion of the rectum, the kidneys, etc. On these various surfaces sensory elements are found among the epithelial cells in the form of neuro-epithelial or end-cells, which sometimes traverse a thick calcified cuticle (aesthetes of *Chiton*, Fig. 24). These elements are particularly numerous in the most exposed parts, such as the cephalic tentacles of Gastropods, the epipodial tentacles of Rhipidoglossa, the pallial tentacles of Lamellibranchs, etc., which therefore have the more special function of tactile organs.

Taste organs in the form of sensory bulbs or cups have been shown to exist in the buccal cavity or round the mouth of several Molluscs. There are several kinds of organs of olfactory or some analogous function; such are the cephalic rhinophores and the pallial osphradia. The rhinophores are situated on the head, and are frequently borne on more or less prominent appendages resembling tentacles (Fig. 163, *t*); or in other cases they have the form of a pit, as in the Cephalopods (Fig. 259, *ol*). The nerve of each rhinophore is supplied by the corresponding cerebral ganglion, and is sometimes partially united to the optic nerve. The osphradia (Ray Lankester) are situated near the entrance to the pallial cavity (Figs. 58 and 89, *os*; 99, XVI.), on the course of the branchial nerve, but sometimes, as a result of specialisation, they are situated on separate ganglia. The osphradia have the form of ridges or pits lined by sensory epithelium, and their function is to test the respiratory fluid. It has been demonstrated, in certain Lamellibranchs at any rate, that the nerve-fibres supplying the osphradia originate in the cerebral ganglia.

The otocysts (de Lacaze-Duthiers) are invaginations of the integuments of the foot. In the Protobranchs (Pelseneer) and in *Mytilus* (List) they are *otocrypts*, that is to say, they are still open invaginations; but in all other Molluscs these organs are closed and contain auditory granules or otoliths suspended in a fluid secreted by the wall of the otocyst, this latter structure being furnished with sensory and ciliated cells. The otocysts, even when they are attached to the pedal ganglia, are innervated from the cerebral ganglia (Koren and Danielssen, de Lacaze-Duthiers, Leydig; Figs. 123, C; 146). They are absent both in the young and adult Amphineura and in the adult stages of various sessile Molluscs. It is through the agency of these organs that the animal is able to perceive disturbances in the surrounding medium, and the resistance offered to the locomotory apparatus: through them the creeping Molluscs preserve their orientation and swimming Molluscs their equilibrium.

The Eyes are normally cephalic structures, one pair in number, symmetrically placed on or at the bases of the cephalic tentacles. Cephalic eyes are absent in the Scaphopods and in the adult state in Amphineura and the Lamellibranchs (with the exception of the Mytilidae and *Avicula*). In Molluscs devoid of cephalic eyes, visual organs are often developed on the mantle. Thus among the Amphineura they are found over the whole surface of the mantle in the Chitons; among the Lamellibranchs on the borders of the mantle only in the Arcidae and in numerous Pectinidae; finally, one

Gastropod, *Oncidium*, possesses, in addition to a pair of normal cephalic eyes, numerous pallial eyes scattered over the whole dorsal surface.

The cephalic eyes are pigmented invaginations of the integument: they may be open, without any refractive body, as in *Patella* and *Nautilus* (Fig. 6, A), or with a crystalline lens, as in *Pleurotomaria*, *Trochus*, *Haliotis*, etc. They are closed, and have a cornea and an internal crystalline lens in the majority of Gastropods and in the dibranchiate Cephalopods (Fig. 6, B, C). The pallial eyes may be "compound," without an internal crystalline lens (Arcidae), or simple. In the latter case they may present one of the following characters:—(1) an internal crystalline lens and a deep retina (Polyplacophora, Fig. 33); (2) an internal crystalline lens and a superficial retina (*Pecten*, Fig. 217); (3) an internal crystalline lens, the retinal cells reversed and the nerve traversing the retina (*Oncidium*). With the exception of the Cephalopods, and possibly also the Heteropods, the vision of Molluscs is limited. In the forms devoid of eyes, as in other groups of the animal kingdom, the general surface of the body is capable of dermatoptic perceptions.

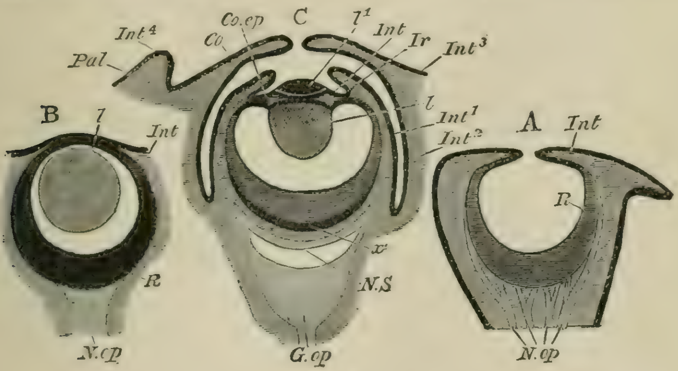

Fig. 6.

Diagrams of sections of the eyes of Mollusca. *A*, *Nautilus*; *B*, Gastropod (*Limax* or *Helix*); *C*, Dibranchiate Cephalopod (Oigopsid). *Co*, external cornea; *Co.ep*, internal cornea; *G.op*, optic ganglion; *Int*, Int^1, Int^2, Int^3, different parts of the integuments; *Ir*, iris; *l*, crystalline lens; l^1, outer (extra-corneal) portion of the lens; *N.op*, optic nerve; *N.S*, nervous stratum of the retina; *Pal*, eyelid; *x*, inner layer of the retina. (From Lankester, after Grenacher.)

7. *Organs of Generation*.—Among Molluscs in general the sexes are separate, and this is the case in the most archaic forms of the different groups of the phylum. Hermaphroditism, on the contrary, is always a sign of specialisation, and is only found as a normal condition in one sub-order of Amphineura (Neomeniomorpha), in one sub-class of Gastropoda (Euthyneura), in some genera of Streptoneura, in one order (Anatinacea), and in some isolated species of Lamelli-

branchia. In the forms with separate sexes there is often a definite sexual dimorphism, which is exhibited not only by the presence of a copulatory organ (Cephalopods and the majority of Gastropods), but also in the breadth and even in the greater size of the females (Fig. 7, *f*). It has been shown that in the Cephalopods hyperpolygyny is the rule, and in certain *Atlantae* and American Unionidae, hyperpolyandry. The gonads are primitively paired and developed from the coelomic wall, but they are only in direct communication with the remainder of the coelom (the pericardium) in the Aplacophora (Figs. 5^{bis}, *d*; 30, C) and the Cephalopoda (Fig. 5^{bis}, *b*). In the former case the genital products fall into the pericardium and are carried to the exterior by the renal ducts, which thus act as gonaducts. In other cases the genital products may be discharged into the reno-pericardial duct (*Trochus*, Fig. 55; *Solenomya*), and are thence expelled through the kidneys, or they may be discharged directly into the kidneys, more or less close to the external renal orifice (various archaic Lamellibranchs, the majority of Rhipidoglossa, Scaphopods). Otherwise, in all groups, the gonads open to the exterior by their proper pores, which are nearly always adjacent to the renal openings; they may, however, be more or less removed to a distance from the latter, and in certain hermaphrodite forms (Pulmonates and Nudibranchs) the renal orifice is near the anus and the genital aperture is secondarily separated from it and shifted towards the penis. Accessory glands are often developed on the course of the genital duct, especially in the female.

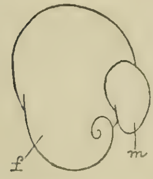

Fig. 7.
Lacuna pallidula. The male *in situ* on the right margin of the shell-aperture of the female. × 2. *f*, female; *m*, male.

The male and female elements are formed from the epithelium of the gonad: each oogonium gives rise to a single ovum with its polar bodies, while each spermatogonium gives rise to several spermatozoa. The eggs of Cephalopods, of the majority of Polyplacophora, and of the Lamellibranch *Pseudokellya* (Fig. 220) are invested by a continuous cellular follicle. In hermaphrodite Molluscs the spermatozoa ripen before the ova; the hermaphroditism is therefore protandric. The hermaphroditism also is not self-sufficient, and the ova of one individual must normally be fertilised by the spermatozoa of another individual. The "parthenogenesis" observed in hermaphrodite Pulmonata (*Arion*, *Limnaea*), which have been isolated from the time of their birth, is possibly due to an abnormal autofertilisation.

"Progenesis" has only been observed in one Gymnosome (*Clione*), in which the larval characters are preserved for a long time. Copulation only takes place in such Gastropods, whether monoecious or dioecious, as are provided with a penis, and in the Cephalopoda. In several members of the latter class the copulatory organ, or hectocotylus, is caducous and travels independently in search of the female. In those Molluscs which do not copulate the eggs are fertilised after oviposition. The eggs are laid separately in the Amphineura, in the more archaic Gastropoda, in the Scaphopoda, and in almost all the Lamellibranchia (that is to say, generally, in the forms that do not copulate), but in the majority of aquatic Gastropods and in the Cephalopods the eggs when laid are united into a gelatinous or coriaceous nidus, which may be attached (benthos) or floating (plankton). As a rule, Molluscs do not nurture their progeny, and when once the eggs are laid they take no further heed of them. Some of them, however, retain their eggs till the time of hatching, and are therefore called incubatory forms (Fig. 8). Examples of incubatory forms occur among the Lamellibranchs, especially the specialised eulamellibranchiate Submytilacea; among marine Gastropods (*Vermetus*, etc.), among freshwater Gastropods (*Melania*, etc.), and even among the octopodous Cephalopods (*Argonauta*), but the number of truly viviparous forms is very small. *Callistochiton* among the Amphineura and several genera of aquatic and pulmonate Gastropods are the only instances.

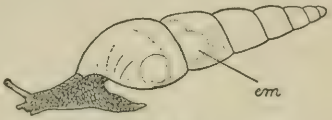

Fig. 8.

Stenogyra mamillata, left side view, with four embryos in the oviduct. *em*, embryo.

The number of eggs laid is very variable. It is always greater in the case of those marine Molluscs which abandon their eggs to the mercy of the waves than in those which deposit them in a nidus, agglomerated together in ribands or in shells in which the embryos are naturally protected. Thus *Ostraea* may lay as many as 60,000,000 eggs, *Chiton* 200,000. On the other hand, numerous eggs are found in the nidus of certain Nudibranchs (50,000 in the case of *Doris*), Cephalopods (*Loligo*, 40,000), and pelagic Gastropods (*Cymbulia*, 1200). In all cases in which numerous eggs are laid free larval forms are developed, but when the whole of the developmental stages are passed through within the egg-membranes, and when the young individual is hatched with the characters of its parents and undergoes no metamorphoses, the number of eggs is generally small (*Cenia*, 4-12), or the greater number of the eggs laid is absorbed and furnishes nutriment for a few embryos (*Buccinum*, *Purpura*, etc.). In the following cases also eggs are laid in small numbers:—(1) In incubatory forms, such as *Vermetus*, where from 120-240 eggs are incubated in the pallial cavity, under the protection of the shell; (2) in terrestrial and fluviatile species, in which the number of eggs is always smaller than in marine forms. In this case caenogenesis or embryonic condensation is the rule; the young animal quits the egg in the adult form, and there is no need for a large number of embryos. Instances in point are—

Limnaea, 20-100 eggs; *Helix*, 40-100; *Ancylus*, 5 or 6; *Valvata*, 17; *Neritina*, 50-60. Lastly, the number of eggs is small in viviparous forms: in *Paludina* there are about 15; in *Subulina* (Fig. 8) there are 4.

III. Embryology.

In the Mollusca the segmentation of the egg is unequal. In some primitive forms, it is true, the first two or three divisions are regular (*Patella*, Fig. 9, A; *Chiton*), and the two first blastomeres are often equal in size, but it is frequently the case that even the first division is unequal (many Lamellibranchs, Rachiglossa, etc.). From the first phases of segmentation up to the blastula stage one may distinguish two kinds of cells or blastomeres: the ectodermic cells, called ectomeres or micromeres; and the endodermic cells, called endomeres or macromeres. In the more primitive forms, however, such as *Patella* (Fig. 9, A), and the Protobranchia, there is scarcely any difference in size between the two kinds of blastomeres, but in proportion as the endodermic cells are charged with food-yolk so does the difference in size become accentuated, as may be seen in the Taenioglossa (Fig. 9, B), and particularly in the Lamellibranchs (Fig. 9, C) and Rachiglossa. In the last-named group the irregularity of segmentation reaches its maximum, leading to the stage of incomplete or meroblastic segmentation characteristic of the Cephalopods (Fig. 9, D). It is quite exceptional for the segmentation to become secondarily regular, as in *Paludina*, where this condition is due to the diminution of the yolk (Fig. 110).

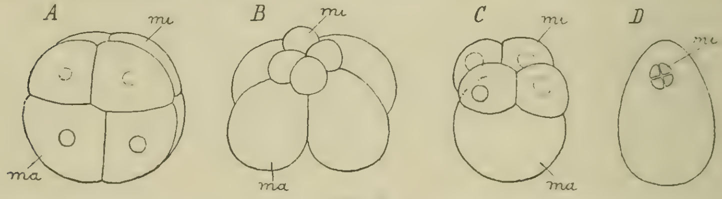

Fig. 9.

Eggs of various Mollusca, at the same stage, with 4 micromeres. *A*, *Patella* (Patten); *B*, *Lacuna*; *C*, *Teredo* (Hatschek); *D*, *Sepia* (Kölliker). *ma*, macromeres; *mi*, micromeres.

The separation of the ectodermic from the endodermic elements of the embryo follows a constant rule, similar to that which obtains among the Annelida. After the formation of the four primary micromeres two new series or quartettes of micromeres are formed at the expense of the large endodermic cells, and all the ectodermic organs are formed from these three quartettes. The micromeres multiply more rapidly than the macromeres, and there are even cases, such as *Dentalium* (Fig. 184), certain Rachiglossa, and Lamellibranchs (*Teredo*, Fig. 9, C, *Cyclas*, Unionidae), in which there is only a single macromere during the early stages of segmentation. The segmentation sphere or blastula is thus formed of two more or less unequal moieties, respectively known as the formative (ectodermic) and nutritive (endodermic) moieties. Internally there is a segmentation cavity or blastocoele, generally much reduced (Fig. 10, A), except in certain Lamellibranchs (*Cyclas*, *Dreissensia*, etc.) and stylommatophorous Pulmonates. The animal or formative pole of the egg is indicated by the presence of the polar bodies; the vegetative or nutritive pole is opposite, and at this point the blastopore or orifice of the digestive cavity will be formed (Fig. 110, A, *bl*).

Formation of the Digestive Cavity and of the Diblastula or Gastrula.—The final result of the segmentation is that the micromeres form a more or less complete envelope to the segmented ovum, covering over the macromeres which remain within to form the endoderm. But the formation of this double-walled sphere, the diblastula or gastrula, may be effected in one or the other of two apparently different methods, invagination or epiboly. Invagination or emboly is certainly the more primitive method, and is realised in ova with a relatively small amount of food-yolk. In this case the nutritive moiety of the blastula is doubled back within the formative moiety, much as one half of a deflated hollow indiarubber ball may be pushed by the finger within the other half. These two halves are separated by a remnant of the original segmentation cavity, which is invariably much reduced by the process. The invagination thus produced gives rise to the digestive cavity or archenteron, lined by the endoderm and communicating with the exterior by the blastopore. As examples of this mode of formation one may cite *Chiton* (Fig. 10, A), *Paludina*, the Pulmonata, the Nudibranchia, the Pteropoda, the Gymnosomata and Limacinidae, the Scaphopoda, *Nucula*, *Ostraea*, *Pisidium*, and the Unionidae.

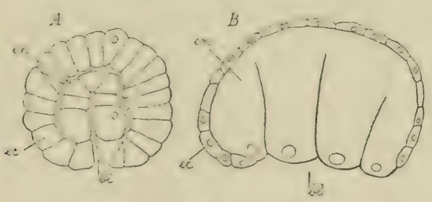

FIG. 10.

Two types of gastrulae. *A*, invaginate or embolic (*Chiton*: after Kowalewsky); *B*, epibolic (*Crepidula*: after Conklin). *bl*, blastopore; *ec*, ectoderm; *en*, entoderm.

The gastrula is formed by epiboly when the nutritive cells or macromeres have become so much distended with food-yolk as to be too large to be invaginated into the layer of micromeres. In such case the micromeres as they multiply grow round the endoderm and gradually surround it, leaving at the nutritive pole an orifice, which is the blastopore. Examples of this mode of formation are—Many streptoneurous Gastropoda (*Trochus*, *Vermetus*, *Crepidula*, Fig. 11, *Janthina*), the majority of the Rachiglossa (*Columbella*, *Fusus*, *Nassa*, *Purpura*, *Urosalpinx*), the Tectibranchs (*Acera*, *Philine*, *Aplysia*, Thecosomata), and many Lamellibranchs (*Pecten*, *Modiolaria*, *Cardium*, *Teredo*, etc.). The two processes, however, differ only in appearance, and there are intermediate stages which form an insensible passage from one method to the other. In fact, complete invagination only occurs when the segmentation is quite or very nearly regular (*Paludina*, *Chiton*, etc., Figs. 10, A, and 110, A), but in consequence of the progressive increase of the amount of food-yolk contained in them, the macromeres become larger and larger and are only able to be invaginated at a late stage of development. That is to say, in certain embolic gastrulae there is a commencement of epiboly, followed eventually by an invagination of the macromeres (*Firoloida*, *Clione*, *Nucula*).

In the various cases enumerated above the segmentation of the ovum is complete or holoblastic. In the Cephalopods the case is different, for the segmentation is incomplete or meroblastic (Fig. 289), a large part of the egg being formed of food-yolk which takes no part in the division. But it must be remarked that in various types, such as the specialised Gastropods (Rachiglossa: *Nassa*, *Purpura*, *Fusus*, etc.; Tectibranchia: *Acera*, *Aplysia*, *Carolinia*, etc.), there is a sort of quasi-distinct yolk, formed by the granular portion of the macromeres. Hence the meroblastic or "discoidal" segmentation of the Cephalopods is not absolutely distinct from the total segmentation observed in other Molluscs: it is only an exaggeration of epiboly. In fact, as the yolk forms the principal part of the ovum and the protoplasm is concentrated at the formative pole, the ectoderm is formed over a limited region of the yolk (the "germinal disc" or "embryonic area"), and is unable to envelop it entirely, so that development proceeds as if the process of epiboly had been left incomplete, the blastopore remaining very large and leaving all that part of the yolk which could not be covered by the ectoderm outside the embryo. Under these circumstances the endoderm is essentially an embryonic tissue, exclusively employed in the constitution of the vitelline mass, and degenerates in the adult, a great part of the digestive tract of the latter, a long stomodaeum and a long proctodaeum, being formed by the ectoderm. The passage to this condition is presented by some Gastropods with an abundant yolk: in *Nassa* a part of the primitive endoderm degenerates in the adult, and in *Fusus* the four macromeres of the primitive endoderm seem to form a provisional embryonic organ, and it is the ectoderm that forms nearly the whole digestive tube. In the different groups of Molluscs the liver is formed from the wall of the enteron, generally as a pair of diverticula given off from its middle region (Fig. 116), and composed exclusively of cells of a fatty nature, while nutrition is effected by the absorption of the yolk.

Formation of the Orifices of the Digestive Tube.—The gastrula mouth or blastopore, at a given period of the development at any rate, has very often the form of an elongated slit. This condition is shown in *Patella* (Fig. 113, III), *Bithynia*, various Opisthobranchs, such as *Aplysia* and Nudibranchs, in basommatophorous Pulmonates, *Cyclas*, etc. This slit gradually closes up from behind forwards, its two margins forming the ventral pedal prominence. In other cases this aperture may be more or less elongated, oval in shape, with an anterior groove running forward as far as the velum, as is seen in *Paludina*. Or again, the blastopore may be circular, and be gradually displaced from behind forwards, suggesting a specialised condition of the slit-like blastopore which closes in the same direction. The linear or circular blastopore is totally closed in a large number of cases; such are, Aspidobranchs: *Patella*, *Trochus*, and *Neritina*; Pectinibranchs: *Bithynia*, *Nassa*, *Purpura*, *Natica*, *Lamellaria*, and *Crepidula*; Opisthobranchs: *Aplysia*, various Pteropods and Nudibranchs; Lamellibranchs: Cyrenidae, Unionidae, *Dreissensia*, *Teredo*. In other forms the blastopore, though it may contract so much as to be scarcely visible, remains open; if it is a linear blastopore it is the anterior end that persists. Examples are, *Chiton*; several marine Streptoneura, including *Vermetus*, *Fusus*, and Heteropods; Pulmonata; *Dentalium*; *Nucula*; *Ostraea*.

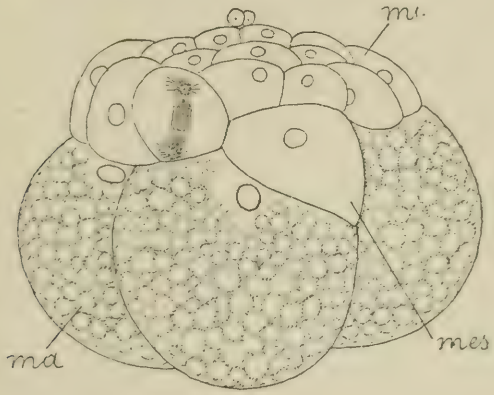

FIG. 11.

Eggs of *Crepidula*, showing the origin of the first mesodermic cell. *ma*, macromeres; *mes*, first mesodermic cell; *mi*, micromeres. (After Conklin.)

An invagination of the ectoderm at the place where the blastopore closed, or surrounding the blastopore if it remains open, places the digestive cavity (enteron) of the gastrula in communication with the exterior. This invagination constitutes the stomodaeum, from which the pharynx and oesophagus with all their accessory apparatus, the salivary glands, radula, etc., are formed. Thus the blastopore, if it remains open, does not become the mouth of the adult. *Paludina*, however, is an exception, in that the whole of the blastopore remains open and becomes the anus (Ray Lankester), whilst the stomodaeum is formed at the anterior end of the embryo (Fig. 110, F, *m*). Later, in Molluscs in general, the proctodaeum is formed as a very short anal invagination, at the posterior end of the original blastoporic groove. Its position is generally indicated by the presence of two prominent ectodermic cells, and it perforates the posterior part of the archenteron, establishing a communication between the intestine and the exterior.

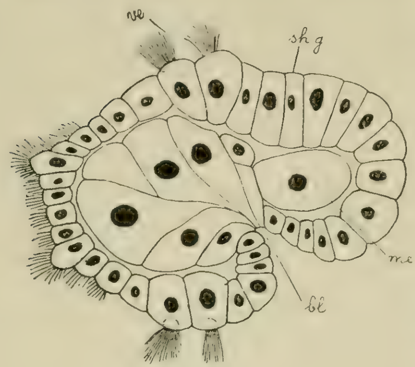

Fig. 12.

Trochosphere of *Patella*, sagittal section. *bl*, blastopore; *me*, mesoderm; *sh.g*, shell-gland; the two dorsal, *ve*, and the two ventral ciliated cells are the velar cells. (After Patten.)

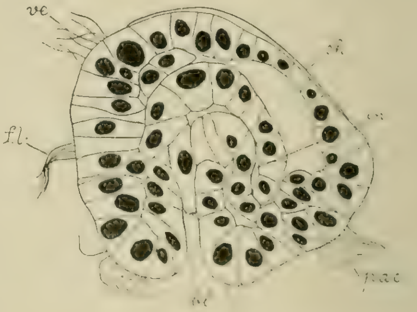

Fig. 13.

Trochosphere of *Dreissensia*, median sagittal section. *bl*, blastopore; *fl*, flagellum; *in*, intestine; *p.a.c*, post-anal cilia; *sh*, shell; *ve*, velum. (After Meisenheimer.)

Ectodermic Organs.—The embryo, then, has an endodermic digestive cavity and a general ectodermic envelope from which the oesophagus and the anal invagination are derived. But the ectoderm is principally concerned in the production of the permanent tegumentary organs properly so called, such as the foot, the mantle, and the ctenidia, and those organs which, although deeply placed, originate from the surface, such as the nervous system and the organs of sensation. The ectoderm further gives rise to the embryonic locomotory organs which result from a special adaptation to larval life. The most important of these embryonic organs is the velum; primitively a preoral ciliated ring, characteristic of the Trochosphere (Ray Lankester), which delimits an area known as the prostomium or "velar area." Towards the centre of this area there is often a ciliated tuft or a flagellum, as in the larvae of Amphineura (Figs. 14, 17), *Patella* (Figs. 14, 113), *Dentalium* (Fig. 15), and various Lamellibranchs (Figs. 14, C; 16). It is on the buccal side of this tuft, when it exists, that the apical plate is situated, probably the remains of a sensory organ from which the cerebral nerve-centres take their origin. The velum may be differentiated in one of two ways:—(1) The preoral ciliated ring may extend itself by growing outwards at all parts of its circumference: the trochosphere larva is thus transformed into a "veliger" (Ray Lankester), a larval form highly characteristic of Molluscs (Fig. 18). The velum may be divided into two lateral lobes (Fig. 18, *v*), which in their turn may be divided into two or three secondary lobes (Fig. 121). (2) The velum may retreat for a greater or less distance towards the posterior end of the embryo, becoming attached to it in such a manner as to form a more or less extensive superficial investment furnished with multiple ciliated rings, as in *Dentalium* (Figs. 15,

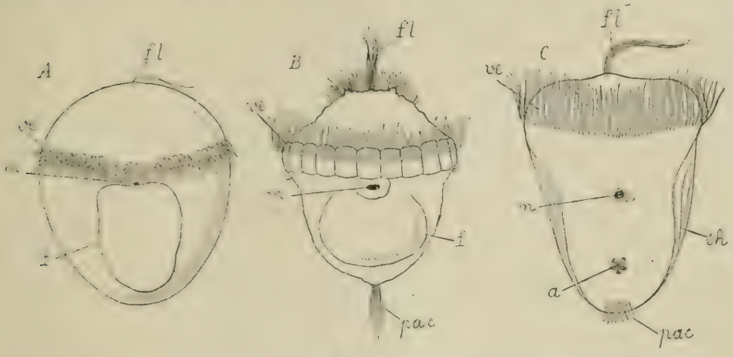

FIG. 14.

Three Trochospheres of Mollusca. *A*, *Ischnochiton* (Heath); *B*, *Patella* (Patten); *C*, *Dreissensia* (Meisenheimer). *a*, anus; *f*, foot; *fl*, flagellum; *m*, mouth; *p.a.c*, post-anal cilia; *sh*, shell; *ve*, velum.

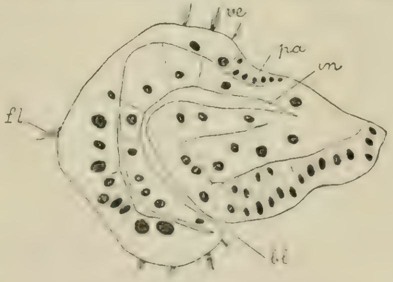

FIG. 15.

Trochosphere of *Dentalium*, sagittal median section. *bl*, blastopore; *fl*, flagellum; *in*, intestine; *pa*, mantle or shell-gland; *ve*, velum. (After Kowalevsky.)

185), Neomeniomorpha (Fig. 17), Nuculidae (Figs. 16, 225). The embryo may in this manner be nearly completely invested by a "test" extending posteriorly to an orifice which, however, is only a false blastopore.

In both cases the velum eventually atrophies when the animal assumes the definitive habits of the adult. When the whole course of the development is undergone within the egg-membranes, there is either no veliger stage (Cephalopods, Figs. 119, D; 257, 290, 291; *Cyclas*, *Entovalva*, etc.) or there is no free veliger, but a more or less rudimentary velum, postero-dorsally atrophied, may be observed, which persists nearly to the time of hatching (viviparous Gastropods, *Purpura*, Fig. 1, Pulmonata).

A post-anal ciliated area is not uncommonly found, as, for example, in *Purpura* (Fig. 1), among Gastropods, and *Dreissensia* (Figs. 13, 14, *p.a.c*) among Lamellibranchs. Finally, post-oral ciliated rings, secondarily acquired, are found in the larvae of certain Opisthobranchs, Gymnosomata (Fig. 120).

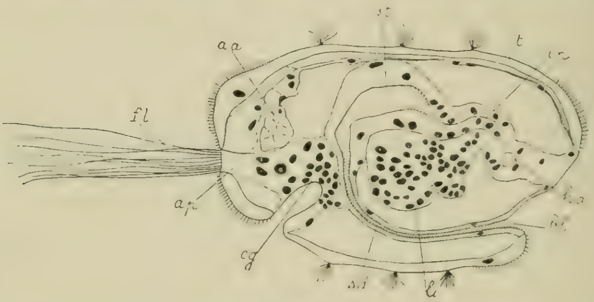

FIG. 16.

Trochosphere of *Yoldia*, median sagittal section. *a.a*, anterior adductor muscle; *ap*, apical plate; *bl*, blastopore; *c.g*, cerebral ganglion; *fl*, flagellum; *h.a*, posterior adductor; *in*, intestine; *li*, liver; *sd*, stomodaeum; *t*, "test" or reflected velum, with 3 circlets of cilia. (After Drew.)

The *foot* is nothing more than a projection of the integument between the mouth and the anus. Its earliest rudiment is evidently paired, since it is formed by the union of the lips of the (commonly) elongated blastopore (Fig. 113). It is only at a late stage of development that it attains its complete development; during the early stages it is very small and functionless, the velum serving as the sole organ of locomotion (Fig. 112).

An ectodermic invagination, bounded by a ridge, makes its appearance at an early period on the dorsal face of the embryo, near the formative pole. This invagination, known as the "shell-gland" (Ray Lankester) or preconchylian invagination (Fig. 110, E, F, *sh.gl*), is also the precursor of the mantle, since the edge of the latter structure is formed by the ridge. The shell-gland spreads from its point of origin in the form of a pallial thickening, which may be only slightly concave, or it may be deeply invaginated and afterwards evaginated. The invagination is caused by the very rapid proliferation of the epithelial tissue in the neighbourhood of the pallial ridge. When evaginated these epithelial cells, having again become external, begin to secrete the shell.

The *branchiae* or *ctenidia* originate on the inner surface of the mantle as tegumentary projections in the form of papillae or of filaments arranged in series (Fig. 229).

The Nervous System and Organs of Sensation.—The various pairs of nerve-centres arise separately, and usually as thickenings of the ectoderm at the points where they are formed. In certain cases, however, the nerve-centres are developed by the more primitive process of invagination, as may be seen in the case of the cerebral ganglia of *Dentalium*, *Vermetus*, *Carolinia* (paired invaginations), *Yoldia* (Fig. 16, *c.g*), and *Dreissensia* (an unpaired invagination), a portion of the cerebral centres in Pulmonates, and the cerebral, pedal, and visceral ganglia of the Unionidae. When the cerebral ganglia are formed by invagination, a single pit, or a pair of pits, is formed on the oral side of the apical plate, from the bottom of which ganglion cells are budded off; the remainder of the invagination goes to form the labial palps, etc., of Lamellibranchs, and probably the rhinophores of Gastropods.

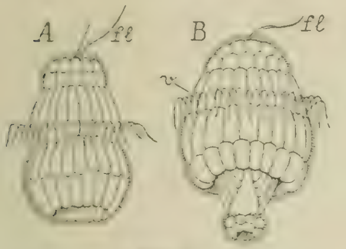

FIG. 17.

Trochosphere of *Myzomenia banyulensis*. *A*, after 36 hours; *B*, after 100 hours. *fl*, flagellum; *v*, velum. (After Pruvot.)

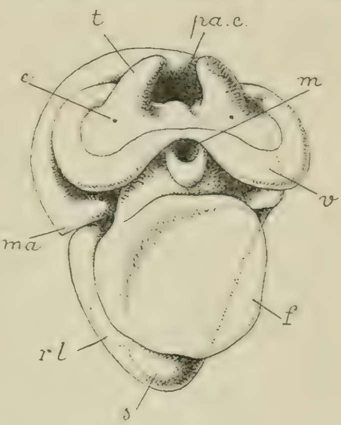

FIG. 18.

Veliger of *Littorina*, ventral view, × 80. *c*, eye; *f*, foot; *m*, mouth; *ma*, mantle; *pa.c*, pallial cavity; *r.l*, right liver lobe; *s*, stomach; *t*, tentacle; *v*, velum.

The eyes also, including the pallial eyes of the Pectinidae, and the otocysts are sometimes developed from ectodermic thickenings; but in many cases these organs are formed by invagination, for example, in various Cephalopoda (Fig. 119, D); in Gastropoda: in the Aspidobranchs, *Paludina*, *Bithynia*, *Calyptraea*, *Crepidula*, *Nassa*, the Heteropoda, and the Pulmonata. The otocysts only are formed by invagination in some other Gastropods (*Fusus*), and in *Dentalium* and various Lamellibranchs.

Mesoderm and Mesodermic Organs.—A third intermediate cellular layer is formed, generally at an early stage, between the external ectodermic envelope and the endodermic wall of the digestive tube. This is the mesoderm, from which all the organs situated between the digestive tube and the integuments are produced. The origin of this layer is often difficult to determine, especially in highly specialised forms, but in all cases in which the origin is distinct there is no doubt about the matter, the mesoderm is derived from the endoderm. This derivation is shown in the Polyplacophora, the Aspidobranchs (*Patella*, Fig. 12, *me*; *Trochus*, *Neritina*), the Pectinibranchs (*Paludina*, *Bithynia*, *Crepidula*, *Fulgur*, etc., and seemingly the Heteropoda), the Opisthobranchs (*Philine*, *Umbrella*, *Aplysia*, *Clione*, *Chromodoris*, etc.), the basommatophorous and stylommatophorous Pulmonates, the Scaphopods, the Lamellibranchs (*Pisidium*, Unionidae, *Dreissensia*, *Teredo*, etc.). Nevertheless we find scattered mesodermic cells, giving rise to unicellular muscular fibres of the integument (*Unio*, *Crepidula*), which are derived from the ectoderm.

The principal result of the development of the mesoderm is the formation of another cavity in the embryo, the coelom. In the Mollusca the coelom does not originate by the invagination of enterocoelic pouches (Tönniges has shown the inaccuracy of Erlanger's description of enterocoelic coelomic pouches in *Paludina*), but, as a result of specialisation, this primitive method is supplanted by solid mesoblastic masses, generally paired, which may be considered as the cardio-genito-renal rudiments. These mesoblastic masses take their origin from the macromeres. As a rule, at the stage when four macromeres are present, it is the most posterior of the four that gives rise, by successive divisions, to the two first mesomeres or primary mesodermic cells (Fig. 11). From these the two mesodermic bands, which constitute the third layer, are produced as solid, or in some cases discontinuous masses. The coelomic cavity or series of cavities are formed by more or less regular fission or delamination of the mesoblastic bands,—evidently a secondarily acquired mode of development. The coelom is therefore physiologically a schizocoele. Eventually it is placed in communication with the exterior by ectodermic invaginations. The order in which the different parts of the primitive coelomic cavity make their appearance is not constant. The pericardium, in particular, may originate as two symmetrical cavities, which unite more or less rapidly (*Paludina*, *Cyclas*, Cephalopoda), or directly, as a single azygos cavity (*Dreissensia*, Pulmonata). The extension of the mesodermic elements evidently narrows the primitive segmentation cavity or blastocoele, which becomes the cavity of the circulatory system. These elements spread between the ectoderm and endoderm, and become specialised to form the internal lining of the circulatory cavity in particular, and may even fill almost entirely the remainder of the blastocoele in the form of a false mesenchyme (caenogenetic or secondary mesenchyme), which constitutes the connective tissue. This naturally restricts the extension of the coelom properly so called, so that it is commonly reduced to the pericardial cavity. Since the mesodermic tissue gives rise, in this manner, to the epithelial wall of the coelomic cavity, to the lining of the circulatory cavity, and to the conjunctive tissue filling up the spaces between the organs, one must recognise it as sharing in the evolution, firstly, of the coelom and the excretory and reproductive organs derived from the coelom; secondly, of the circulatory apparatus—the heart, etc.

The coelom, of which the formation has been described above, is essentially a cavity communicating with the exterior, and its epithelial wall may be differentiated in two special ways—into excretory or renal elements, and into reproductive, and therefore caducous elements. In the most primitive process the kidneys are formed in connection with a portion of the coelom, with which they remain in complete continuity (*Paludina*). In other cases they are formed by a hollowing out of a portion of the mesoderm in contact with the pericardium (*Bithynia*, *Limax*, *Cyclas*, *Dreissensia*, etc.), or they may be formed independently in their definitive position (Cephalopoda). Eventually each kidney acquires a communication with the pericardium, and in all cases makes a connection with the exterior by an ectodermic invagination. The genital organs or gonads originate either from the wall of the coelom or pericardium (*Paludina*, *Dreissensia*), or in contact with the coelomic wall (*Cyclas*), or from a rudiment common to themselves, the pericardium and the kidney, or, finally, from distinct mesodermic elements. The continuity of the pericardium and gonads is well preserved only in the Aplacophora (Fig. 30, C) and adult Cephalopoda (Fig. 252, *cor*); in all other Molluscs the genital organs are separated from the pericardial cavity and acquire communications either with the kidneys or directly with the exterior. In the latter case the terminal portions of the gonaducts, together with the accessory genital glands, are ectodermic in origin.

The heart may arise from a portion of the wall of the pericardium itself (*Paludina*), or a common rudiment may give rise to the wall of the pericardium and the heart (Pulmonata, *Cyclas*, *Dreissensia*, etc.), and in the latter case the origin of the heart may be paired (*Cyclas*, Cephalopoda) like that of the pericardium itself.

The larvae of such Molluscs as lay their eggs singly and free in the sea are hatched out very rapidly; a few hours suffice in the case of *Dentalium* among the Scaphopoda; twenty hours in *Trochus* among the Aspidobranchs; fourteen hours in *Yoldia* among the

Lamellibranchs; twenty-four hours in *Pholas*, etc. The eggs of *Gleba*, aggregated into a nidus, are hatched after three or four days, those of *Ischnochiton* after seven days; but in the majority of Gastropods and the Cephalopods the time required is much longer. The marine larvae of temperate seas are intolerant of a rise of temperature, and generally perish when it approaches 30° C.

IV. Definition of the Mollusca.

From what precedes, it results that in each of the five classes the same lines of specialisation may be observed—viz. the loss of the shell, of the foot, of the ctenidia, of the radula, etc. Thus the general morphological characters are obviously those of the most primitive of the different classes (Fig. 19), and the following diagnosis may be proposed for the phylum:—

1. The Mollusca are originally bilateral organisms, in which signs of primitive segmentation are no longer evident.

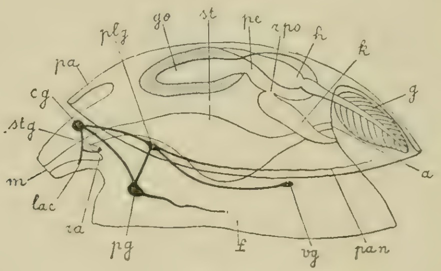

Fig. 19.

Scheme of a primitive Mollusc, viewed from the left side. *a*, anus; *c.g*, cerebral ganglion; *f*, foot; *g*, gill, in the pallial cavity; *go*, gonad; *h*, heart; *k*, kidney; *la.c*, labial commissure; *m*, mouth; *pa*, mantle; *pa.n*, pallial nerve; *pe*, pericardium; *p.g*, pedal ganglion; *pl.g*, pleural ganglion; *ra*, radula; *r.p.o*, reno-pericardial orifice; *st*, stomach; *st.g*, stomato-gastric ganglion; *v.g*, visceral ganglion.

2. They possess a well-developed coelom (gonad and pericardium), enteron, and haemocoel, quite distinct from one another.

3. The alimentary tract exhibits (or has lost) a radular sac in its anterior part.

4. The nervous system consists of a peri-oesophageal ring, whose supra-oesophageal (or dorsal) moiety is the cerebral commissure, and the infra-oesophageal (or ventral) moiety is the labial commissure. The former gives off chiefly sensorial nerves, the latter nerves to the digestive tract. From their union two nervous cords arise on each side, a dorsal or pallial and a ventral or pedal; from the former arise the visceral nerves, whose main trunks are frequently joined together under the digestive canal to form the infra-intestinal visceral commissure.

5. The general body-wall is differentiated into three regions:

(1) the antero-dorsal or cephalic, on which are borne most of the special sense-organs; (2) the postero-dorsal or pallial, which forms a projecting fold around the body, and secretes on its external face a calcified cuticle or shell, and on its lower surface develops respiratory organs or ctenidia; (3) the ventral or pedal, which is the organ of locomotion.

6. A so-called "veliger" or free trochosphere larva is nearly always present in embryonic development; its preoral ciliated ring grows out to form a natatory velum, and at its formative pole there is a "preconchylian invagination" or shell-gland.

V. BIONOMICS AND DISTRIBUTION.

Molluscs are essentially aquatic animals, but the most varied modes of existence may occur, even among members of the same class. The majority are inhabitants of the sea; a few live in fresh water; a single order of Gastropods and a few isolated members of the same group are adapted to a terrestrial life. They are represented in the three great groups of aquatic organisms, namely, in the Benthos, comprising creeping or fixed animals inhabiting the depth of the sea; the Necton, comprising animals that swim actively and can make headway against the currents; the Plankton, comprising animals that float passively and cannot contend with the currents. The first group includes the littoral and abyssal Molluscs, among which the Necton is also represented. The two other groups include the pelagic Mollusca, the Cephalopods belonging exclusively to the Necton, while the free-swimming Gastropods, and those which inhabit pelagic Algae, some isolated Lamellibranchs (*Planktomya*), and the larvae of various groups belong to the Plankton.

The Mollusca are distributed over the whole surface of the earth and in all latitudes. Terrestrial forms are found on the highest mountains—some Stylommatophora at a height of 15,000 feet; lacustrine forms (*Limnaea*) are found at a depth of 350 fathoms. The pelagic forms are not only distributed over the surface of the sea, but may descend to a depth of 2600 fathoms without reaching the bottom. Abyssal Molluscs are found in all oceans extending to a depth of 2800 fathoms from the surface.

As a rule, Molluscs are free-living animals, and crawl, swim, or burrow, but some are sedentary in adult life. Only a few Gastropods and Lamellibranchs are fixed to their habitat. Their modes of alimentation are various. Some are commensal with Ascidians, *e.g. Modiolaria*; some with Echinoderms, as *Montacuta*, *Lepton*, and *Scioberetia*; some with Crustacea, *Lepton squamosum* and *Ephippodonta*, or with Sponges (*Vulsella*), or Annelids (*Cochliolepis*). Others again are ectoparasitic on Echinoderms, such are *Thyca* and

Stylifer (Fig. 20); or, like *Eulima* and *Entovalva*, are endoparasitic, also in Echinoderms. In the latter case the animal may become so degenerate in the adult state as to consist of little more than a sac containing the genital products, as for example *Entosiphon* (Fig. 21), *Entocolax* (Fig. 138), *Entoconcha* (Fig. 139), and *Enteroxenos* (Fig. 140).

There are many cases of protective adaptation and mimicry in the various groups of Mollusca. The pelagic species are generally transparent and colourless or tinged with blue, but the most remarkable examples of mimicry are found among the forms unprotected by a shell (Nudibranchs, *Lamellaria*, etc.), in which the individual assumes the colour and aspect of its habitat, as for instance *Hermaea dendritica* on green algae, and *Hermaea bifida* on *Griffithsia*, a red alga, etc. The abyssal Molluscs are colourless, and are characterised by the thinness of the shell, the atrophy of the visual organs, and the development of tactile organs.

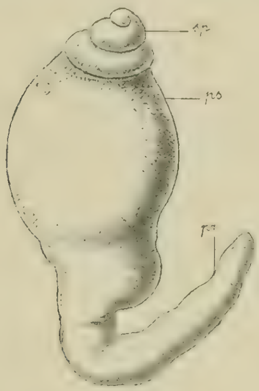

FIG. 20.

Stylifer celebensis, × 12. *pr*, proboscis; *ps*, pseudopallium; *sp*, spire of the shell not covered by the pseudopallium. (After Kükenthal.)

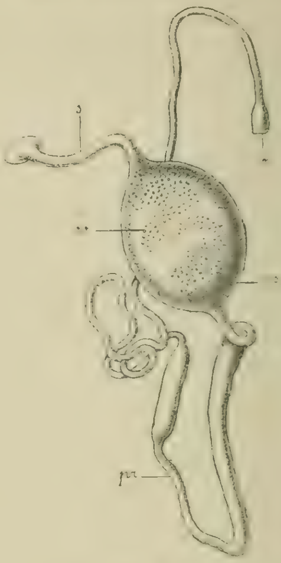

FIG. 21.

Entosiphon deimatis, × 2. *o*, orifice of the proboscis; *ov*, ova; *pr*, proboscis; *ps*, pseudopallium; *s*, fixative siphon. (After Koehler and Vaney.)

Examples of convergence of form may also be noted, such as *Marginella* and *Pseudomarginella* among Gastropods, *Pholas candida* and *Petricola pholadiformis* among Lamellibranchs.

The duration of life in individual Molluscs is ordinarily rather short. Marine Streptoneura may live for several years, and *Littorina littorea*, when in captivity, has attained an age of nearly twenty years. Freshwater Molluscs may live for eight years (*Paludina*).

The Pulmonata are generally biannual, but *Helix pomatia* may attain an age of six years. The majority of Nudibranchs and Tectibranchs appear to live for one year only. Many Lamellibranchs (*Mytilus*, *Teredo*) are adult at the end of one year; Avicula is adult at the end of two years; *Ostraea edulis* is sexual at two years, becomes adult in five years, but may live for ten years in oyster-beds. The huge *Tridacna* lives for about eight years, the Cyrenidae only two years, but the Anodontidae are remarkable for their longevity; they do not become sexually mature till they are five years old, and they continue to grow to the age of twenty or thirty years. In the Cephalopoda it seems that *Rossia* does not live for more than a year, and *Octopus* not more than four years.

Many Molluscs are able to fast for a long time. Cold affects them less than heat. *Helix* has been known to survive a temperature of – 120° C., and small Gastropods live in thermal springs at a temperature of 42° C. Molluscan embryos and larvae generally perish, in temperate climates, at temperatures of + 31° C. and – 3° C.

Descriptive zoologists have enumerated more than 28,000 species of living Molluscs, of which more than half are Gastropods. Fossil representatives of Molluscs are found in all deposits from the Palaeozoic onwards.

1. *Distribution in Space.*

I. *Marine Molluscs* — A. *Littoral Fauna.*—The shores of continents are divided into three provinces by great thermal variations. α. The North Polar province, with characteristic genera such as *Cryptochiton*, *Mölleria*, *Lacuna*, *Velutina*, *Onchidiopsis*, *Solariella*, *Machaeroplax*, *Volutharpa*, *Torellia*, *Cyprina*, *Mya*. β. The South Polar province, with the characteristic genera *Photinula*, *Struthiolaria*, *Cominella*, *Eatoniella*, *Cyamium*, *Lissarca*, *Philippiella*, *Modiolarca*. γ. The tropical province, or region of coral reefs, in which one may distinguish four sub-regions:—(1) The Indo-Pacific, the home of *Nautilus* and the chief forms of the Toxiglossa. The Mediterranean should be included in this sub-region, and the Australo-Zealandic division of it, just as is the case with the terrestrial fauna, presents special characters, as shown in *Trigonia*, *Amphibola*, etc. (2) The West African and (3) the East American sub-regions, which have several forms in common. (4) The West American, characterised by such genera as *Monoceros*, *Concholepas*, etc. Occasionally species may be naturally or artificially acclimatised in various parts of these regions, but exchanges are only definitively effected between similar latitudes, as for example *Littorina littorea* between Europe and North America, and reciprocally *Venus mercenaria* and *Petricola pholadiformis*.

B. *The Abyssal Fauna*, is not divisible into distinct provinces, and many of its species are universally distributed either in the northern and southern parts of the same ocean or in several different oceans. Thus *Limopsis aurita*, *Semele profundorum*, *Verticordia deshayesiana*, *Arca pteroessa* are found in the Atlantic and Pacific; *Hyalopecten pudicum* and *Silenia sarsii* are common to the Atlantic and Indian oceans. Characteristic abyssal genera are *Leptochiton*, *Scissurella*, *Margarita*, *Cyclostrema*, *Setia*, *Leda*, *Bathyarca*, *Limopsis*, *Hyalopecten*, *Dacrydium*, *Callocardia*, and Septibranchs in general.

C. *The Pelagic Fauna.* — α. The superficial forms are very widely distributed, but may nevertheless be described as belonging to polar and tropical provinces. The North and South Polar fauna are different: to the former belong *Clione limacina*, *Limacina helicina*; to the latter *Spongiobranchaea australis*, *Limacina antarctica*. β. The zonary or deep forms are probably more universally distributed, but are still imperfectly known; they include the luminous Cephalopoda.

II. *Land and Freshwater Molluscs.*—It is only a small number of groups that have quitted the sea to assume a freshwater or terrestrial existence, and among these no Amphineura nor Scaphopoda nor Cephalopoda are found. Among the Lamellibranchs only a few families are found in fresh water, viz. Cyrenidae, *Dreissensiidae*, *Unionidae*, *Aetheriidae* (none of them primitive in organisation), and a few isolated types. Among the Gastropods we find very few Rhipidoglossa, *Neritina*, *Hydrocaena*, *Titiscania*; chiefly Taenioglossa, *e.g.* the *Valvatidae*, *Paludinidae*, *Ampullariidae*, *Hydrobiidae*, *Melaniidae*: some isolated types of Rachiglossa, and practically no Opisthobranchs. As for the terrestrial Mollusca, there are only a few families of streptoneurous Gastropods (Helicinidae, Cyclophoridae, etc.), and the whole order of Pulmonata. Of the last-named, one sub-order, the Basommatophora, has returned to an aquatic life, chiefly in fresh water, but retains for the most part a pulmonary respiration.

It is mostly in warm regions, and particularly in those in which the sea is inclined to be brackish, that marine forms have penetrated into fresh waters. Certain inland seas also have become separated from the ocean, and have preserved a fauna which is partly of marine origin. Lakes Baikal and Tanganyika appear to belong to this category.

The tropical regions in general are characterised by terrestrial forms, such as *Vaginula*, *Helicina*, *Ampullaria*, etc. *Chilina* and *Bulimus* belong to the Neotropical region. *Clausilia* is not found in North America, and, generally speaking, the Pulmonates with folded branchiae are absent from the New World. The Ethiopian province is the home of *Achatina*; the Australo-Zelandic of *Janella*, *Rhytida*, *Vanganella*, *Latia*: the Oriental region of *Cyclophorus* and the Rathouisiidae. The distribution of terrestrial and fluviatile

Molluscs shows that the Asiatic and Australian regions are separated not by Wallace's line, but by another line farther east.

2. *Distribution in Time.*

The five classes of Molluscs were already differentiated at a remote epoch of the Palaeozoic era. The Polyplacophora, the Cephalopoda, and *Dentalium* were represented in the Ordovician; the Rhipidoglossa and the Palaeoconchs (Lamellibranchia allied to *Solenomya*), in the Cambrian.

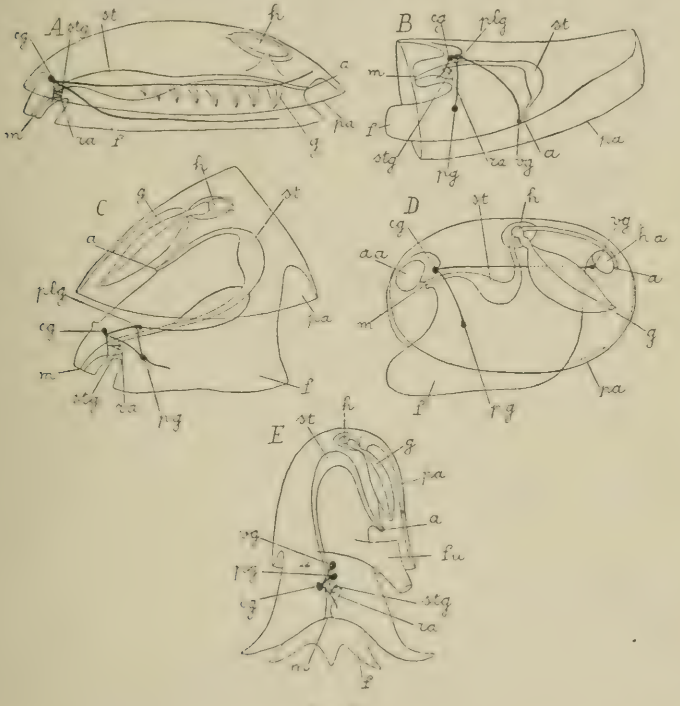

FIG. 22.

Diagrams of the five classes of Mollusca, from the left side. *A*, Amphineura; *B*, Scaphopoda; *C*, Gastropoda; *D*, Lamellibranchia; *E*, Cephalopoda. *a*, anus; *a.a*, anterior adductor; *c.g*, cerebral ganglion; *f*, foot; *fu*, funnel; *g*, ctenidium; *h*, heart in the pericardium; *h.a*, posterior adductor; *m*, mouth; *pa*, pallium or mantle; *p.g*, pedal ganglion; *pl.g*, pleural ganglion; *ra*, radula; *st*, stomach; *st.g*, stomato-gastric ganglion; *v.g*, visceral ganglion.

On the other hand, many ancient stocks have left no surviving descendants. But the appearance of existing genera or families supports the phylogenetic conclusions drawn from the study of comparative anatomy. Among the Cephalopoda it is the Tetrabranchs that appear in the Ordovician; the Ammonites appear only in the Devonian, and the Dibranchs (*Belemnites*) at the beginning of the Secondary. But at the present day all the species of Tetrabranchs, some 7500 in number, are only represented by a few species of the single genus *Nautilus*; and as for the group of Belemnites, it has entirely disappeared since the end of the Cretaceous, its sole surviving and more or less distant representative at the present day being the genus *Spirula*.

Among the Gastropods the Aspidobranchs (Rhipidoglossa) are the first to appear; several families, such as the Capulidae and Pyramidellidae, date back to the Upper Silurian. On the other hand, there are but few Ctenobranchs in the Palaeozoic; most of the families of this order make their appearance in the Secondary, and the same may be said of the Opisthobranchs, with the exception of the Actaeonidae, which are found, as also are the Pulmonata, in the Carboniferous. Of Lamellibranchs various Protobranchs and Filibranchs are found in the Silurian, but the other groups, as a rule, do not appear till the Secondary. The Palaeoconcha of the Primary, and the Rudistae, Diceratidae, Monopleuridae, and Caprinidae of the Secondary, have died out without leaving descendants.

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CHAPTER II

THE AMPHINEURA

CLASS I.—AMPHINEURA, von Jhering (1876)
(= Isopleura, Ray Lankester ; Aculifera, Hatschek).

- Order 1. **Polyplacophora** (Chitones).
  - Sub-Order 1. **Eoplacophora.**
    - Family 1. **Lepidopleuridae.**
  - Sub-Order 2. **Mesoplacophora.**
    - Family 2. **Ischnochitonidae.**
    - ,, 3. **Mopaliidae.**
    - ,, 4. **Acanthochitonidae.**
    - ,, 5. **Cryptoplacidae.**
  - Sub-Order 3. **Teleoplacophora.**
    - Family 6. **Chitonidae.**
- Order 2. **Aplacophora.**
  - Sub-Order 1. **Neomeniomorpha.**
    - Family 1. **Lepidomeniidae.**
    - ,, 2. **Neomeniidae.**
    - ,, 3. **Proneomeniidae.**
    - ,, 4. **Parameniidae.**
  - Sub-Order. 2. **Chaetodermomorpha.**
    - Family 5. **Chaetodermatidae.**

Historical.—The Chitones were formerly the only known forms of this group, and for a long time they were placed in the Gastropoda, near the genus *Patella*, the two forming the Order Cyclobranchia of Cuvier. When *Chaetoderma* and *Neomenia* were investigated from an anatomical point of view, von Jhering united them to the Chitones (1876), and placed the two in a division of "Worms," which he called Amphineura. But the molluscan nature of these Amphineura is so clear, that they were reintroduced into the phylum Mollusca by Spengel, Hubrecht, Lankester, etc., and even von Jhering has since admitted this interpretation. Although Gegenbaur and Claus have again separated *Chaetoderma* and *Neomenia* from the Chitones, and placed the former in a distinct class ("Solenogastres"), and the latter once more in the Gastropoda, the unity of the Amphineura, as well as their molluscan nature, is now very generally accepted.

Definition.—The Amphineura are a group of Mollusca characterised, firstly, by their more or less elongated and quite symmetrical body, with the mouth and the anus situated at its two ends; and secondly, by their mantle, which is always provided with numerous spicules embedded in a cuticle.

General Description.—The mantle is very large, and always covers at least the dorsal surface and the sides of the body. The whole external symmetry reappears in the various internal organs. In the nervous system there are, on each side, two longitudinal cords (one pedal, one pallial) with ganglionic cells along their whole extent. They are united with one another in front, where there is a supra-oesophageal cerebral commissure. The two pedal cords are also united by anastomoses, and in addition each of them also exhibits anastomoses with the corresponding pallial cord. The two pallial cords are united by a thick posterior commissure on the dorsal side of the rectum. There are no otocysts. The buccal cavity is very generally provided with a radula (but mandibles are only present in a species of *Chaetoderma*). The anus and renal orifices are posterior. The heart is dorsally situated in the hind part of the body, and its ventricle is more or less intimately united to the dorsal wall of the pericardium.

All the Amphineura are marine in habit. They are found in all oceans and at nearly all depths. They existed in very ancient geological ages, for they are already present in the Ordovician (Lower Silurian).

There are two very distinct Orders of Amphineura: (1) the *Polyplacophora*, (2) the *Aplacophora*.

ORDER 1. **Polyplacophora**, Blainville.

Definition.—Amphineura, whose chief characteristics are (1) the foot, occupies the whole ventral face of the body; (2) the mantle, bears eight transverse calcareous plates; (3) between mantle and foot there is on each side a more or less complete row of branchiae.

I. GENERAL DESCRIPTION AND EXTERNAL CHARACTERS.

The mantle covers the whole body on the dorsal side; its ventral extension is inversely proportional to that of the foot, and all around the latter there is a pallial groove. The mantle secretes a shell consisting of eight plates or valves articulated with one another and arranged in longitudinal series. Each of these valves partially overlaps the following, except in some species of *Cryptoplax* (= *Chitonellus*), in which the three hindermost are isolated. This articulation of the valves allows the animal to roll up. The two terminal (first and eighth) valves are semicircular, the six intermediate are quadrangular. They may be partially (*Cryptoplax* and some species of *Acanthochiton*) or even wholly (in adult *Cryptochiton*, but not in young ones) concealed by a reduplication of the mantle.

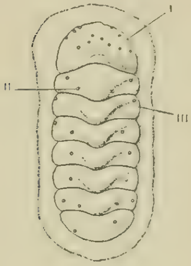

Fig. 23.

Young *Tonicia fastigiata*, Gray, dorsal aspect, showing the first shell-eyes. I, first shell-plate; II, the first eyes on the second shell-plate; III, third shell-plate.

Each valve is made up of two quite dissimilar calcareous layers: (*a*) the uppermost or tegmentum, which alone is visible externally; (*b*) the deeper layer or articulamentum, which is porcellaneous, quite compact, and invisible in the living animal. In most of the lower Polyplacophora these layers are coextensive and have smooth edges, but in the higher forms the articulamentum projects beyond the outer layer into the substance of the mantle, to which it is firmly attached. These projections of the outer or peripheral margins of the valves are termed "insertion plates"; they are generally slit or notched to form the so-called "teeth," which may be either smooth and sharp along the edge or crenulated. The anterior margin of each valve, except the first, is invariably provided with two projections called "sutural laminae," which underlie the hind margin of the valve next in front.

The tegmentum has no representative in the shells of other Mollusca. It is formed by the fold of the mantle covering the edge of the articulamentum, and, as it grows in width, it extends over the latter. It is much reduced in *Acanthochiton* and aborted in the adult *Cryptochiton*. The stratified layers of the tegmentum are traversed by a system of numerous, nearly parallel, ramified canals through which special sense-organs pass to the surface (Fig. 24).

Nearly the whole of the peripheral part of the mantle or "girdle," as it is called, is covered with chitinous or calcareous spicules of various shape, acicular or squamose. Each spicule rests on an epidermic papilla and is formed by a single matrix cell.

The head is more or less cylindrical, consisting of a short downwardly curved snout with the mouth at its extremity. On either side of the mouth is a somewhat angular labial palp. A narrow furrow separates the head from the foot. The latter forms a ventral creeping surface, extending the whole length of the body from head to anus. The breadth of the foot is inversely proportional to the width of the lower edge of the mantle: it is broad in most of the Polyplacophora, but narrow in the Cryptoplacidae.

Extending all round the foot, between it and the mantle on the ventral side, is the pallial groove, in which lie the gills. In the more primitive Chitons mucous thickenings extend into the groove, reaching from the anus to its upper corner, or to the foot, or even to the inner wall of the mantle.

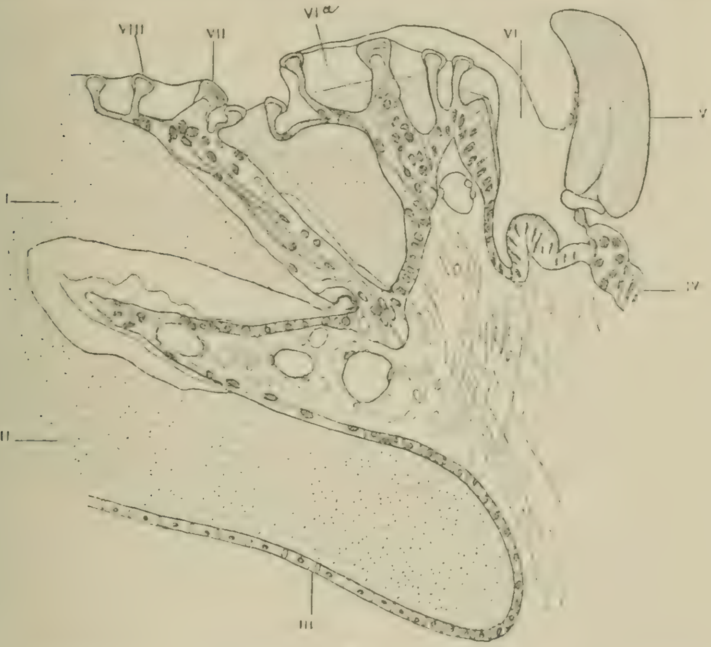

Fig. 24.

Transverse section of the lateral portion of the pallial teguments of *Chiton*. I, tegmentum; II, articulamentum; III, pallial epithelium under the shell; IV, epithelium of the margin of the mantle; V, spicula; VI, cuticle of the mantle-margin; VI*a*, periostracum; VII, megalaesthetes; VIII, micraesthetes. (After Blumrich.)

II. Anatomy.

1. *The Alimentary Canal* extends from one extremity of the body to the other. The mouth leads into the buccal cavity, on the ventral wall of which opens the radular caecum. The radula is long and reaches nearly as far back as the stomach. Each radular row includes seventeen teeth of various shape (Figs. 2, A; 74, E). The three central teeth are simple: on each side of them is a large

recurved thick and dark lateral tooth. Externally are six polygonal marginal teeth: of these the third differs from the rest, being more or less narrow, elongated, and curved, and sometimes its concave edge is ciliated (*Trachydermon*). The fore part of the radula rests upon a cartilaginous mass, moved by a great many muscular bundles.

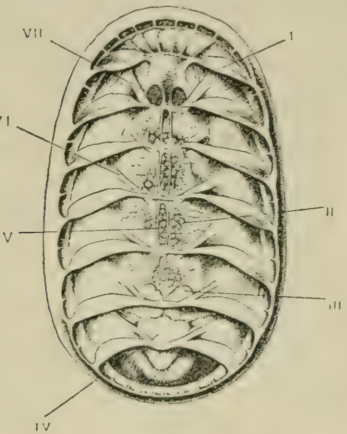

FIG. 25.

Boreochiton cinereus, dorsal view of a female, without the shell-plates. I, first "intersegmentum"; II, ovary; III, oviduct; IV, ventricle of heart; V, dorsal right muscle; VI, dorsal oblique shell-muscle; VII, retractor muscle of the radula.

Two pairs of glands open into the buccal cavity. The true salivary glands lie at the sides, well forward, but behind the cerebral commissure; they are slightly branched, but rather short, and have a very short duct. On the ventral wall, under the subradular organ, lie two very small mucous glands close to one another and to the middle line. On either side, at the point where the pharynx passes into the short oesophagus, is the opening of the sugar gland—a large glandular pouch with a papillose internal surface. The large and thin-walled stomach is surrounded by the liver mass. The two liver lobes are symmetrical in young Chitons, but become asymmetrical in the adult, the right lobe being the smaller and anterior. They open into the stomach either by two distinct orifices (*Chiton aculeatus*), or by two orifices in a single duct (*Lepidopleurus*), or by a single aperture (*Hanleya*). The intestine is very long, as is usual in phytophagous animals, and is thrown into numerous

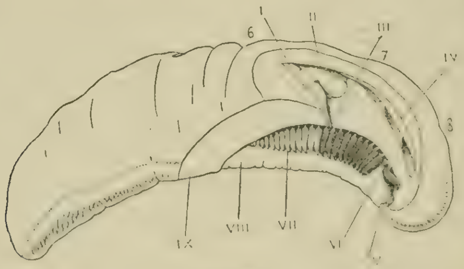

FIG. 26.

Cryptoplax larvaeformis, left-side view, the posterior end partially opened. I, gonad; II, genital duct; III, genital pore; IV, ventricle of heart; V, anus; VI, renal pore; VII, gills; VIII, foot; IX, mantle; 6, 7, 8, position of the sixth, seventh, and eighth shell-plates.

coils. The anus opens at the posterior extremity of the body, between the mantle and the foot (Fig. 28, *a*).

2. *Circulation and Respiration.*—The heart, enclosed in a large pericardium, occupies the postero-dorsal region of the body. It consists of a median elongated ventricle and two elongated symmetrical auricles. The openings of the auricles into the ventricle are subject to some variation. In the Lepidopleuridae, the Mopalidae, and *Tonicella*, *Trachydermon*, *Boreochiton*, etc., among the Ischnochitonidae, the auriculo-ventricular aperture on either side is single and anterior (Fig. 27); in the Acanthochitonidae, the Cryptoplacidae, and the Chitonidae generally there are two apertures on either side (Figs. 4 and 26); in *Chiton squamosus* there are three, and in *Chiton goodalli* four. The auricles are united to one another posteriorly, but there is never a posterior median auriculo-ventricular opening. The posterior auriculo-ventricular orifices are frequently asymmetrical. A single anterior aorta rises from the ventricle anteriorly and carries the blood to the various organs and intervisceral blood-spaces. The venous blood from the different parts of the body is conducted back to a large sinus on either side near to the line of union of the mantle with the body. Closely connected with this same line of union on either side is a row of gills, situated between the foot and the mantle. The number of pairs of gills varies from four in *Lepidopleurus pagenstecheri* to eighty in *Acanthopleura spiniger*, but a careful comparison shows that the number of gills in the right hand row does not always correspond with that in the left.

The gill-rows may be either of the holobranchial type, in which case they extend over the whole length of the body, or of the merobranchial type, in which they are confined to a more or less limited space at the posterior end of the body (Fig. 28). But these two types are connected by transitional forms, and they are not, generally speaking, characteristic of natural groups, nor are they determined by the greater or less size of the species. The genera with few gills are naturally merobranchial, and in the Lepidopleuridae these organs are confined to the region covered by the two last shell-valves. The gills are inserted at the bottom of the pallial groove. The largest gill, which is also the last one in those forms in which no adanal gills are present, is always the first

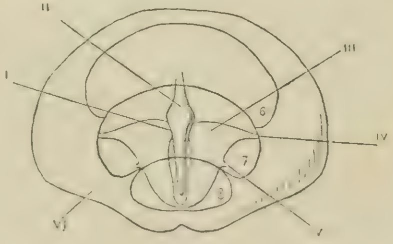

FIG. 27.

Heart of *Mopalia*, dorsal aspect. I, auriculo-ventricular communication; II, ventricle; III, right auricle; IV and V, afferent vessels; VI, mantle; 6, 7, 8, indicate the position of the sixth, seventh, and eighth shell-plates.

behind the renal opening: it is the first to be formed and is the starting-point from which the rest of the gills are added either forwards or both forwards and backwards. Occasionally individual gills may be bifurcated or trifurcated. Each gill has the typical ctenidial structure, consisting of an axis bearing an anterior and a posterior row of gill-lamellae or filaments. The blood from the above-mentioned longitudinal vessel is distributed to each gill by an afferent vessel running along the internal or pedal margin of the axis, and, after being oxygenated in the lamellae, is carried back by an efferent vessel running along the external or pallial edge of the axis to another longitudinal vessel which conducts it back to the corresponding auricle.

3. *Excretory Organs.*—There are two symmetrical kidneys, whose relations were first discovered by Sedgwick. Each of them consists of an elongated renal canal, situated on the lateral side of the visceral mass, and once folded on itself, so that its two ends are posterior. The internal or dorsal end opens into the pericardial cavity, through a ciliated aperture or funnel. The external or ventral end opens to the exterior, between two of the gills at the hinder part of the body. The renal canal is dilated immediately behind its external opening. It is excretory throughout its length, and the excretory surface is increased by numerous small much-branched caeca which lie close to the body-wall laterally and ventrally and open into the canal (Fig. 29).

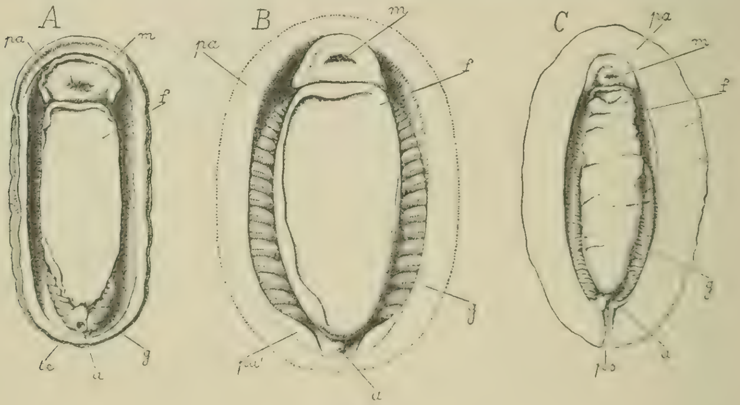

FIG. 28.

Ventral aspect of three species of Polyplacophora, showing the various sorts of gill-rows. *A*, *Lepidopleurus benthus*; *B*, *Boreochiton cinereus*; *C*, *Schizochiton incisus*. *a*, anus; *f*, foot; *g*, gills; *m*, mouth; *pa*, mantle; *pa'*, anal lobe of the mantle; *p.s*, pallial slit; *te*, pallial tentacles.

Various kinds of kidneys are to be found (Plate). They generally extend more or less forwards, and their extension is generally correlated with that of the branchial row. The two branches of the renal canal may be fused together from before backwards until, as in *Callistochiton* and *Nuttalochiton*, the kidney has the form of a simple sac with more or less numerous arborescent appendages, and the pericardial and external apertures adjacent to one another at its hinder end. A similar form of specialisation may be seen in the kidneys of Lamellibranchs. The renal canal may be complicated by the addition of two accessory longitudinal branches, an anterior larger and a posterior smaller, which lie in the foot near the middle of the body.

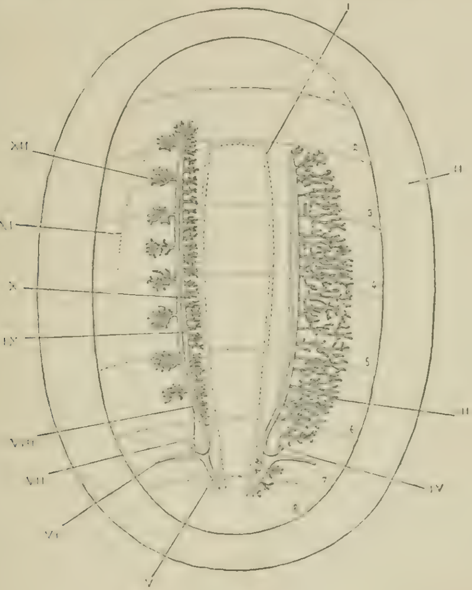

FIG. 29.

Renal organs of *Borcochiton cinereus*, dorsal aspect; on the right-hand side, the exterior ramifications of the antero-posterior renal part are alone drawn; on the left-hand side, all the other ramifications are drawn. I, pedal cord; II, mantle; III, external ramifications of the antero-posterior (or terminal) renal part; IV, reno-pericardial orifice; V, posterior point of the urinary chamber; VI, external renal pore; VII, urinary chamber; VIII, postero-anterior (or initial) portion of the kidney; IX, antero-posterior (or terminal) portion of the kidney; X, internal ramifications of the antero-posterior portion of the kidney; XI, left outer limit of III; XII, ramifications of the initial portion of the kidney; 1-8, the eight "segments" of the body.

4. *Nervous System and Sense-organs.*—There is no concentration of nerve-ganglion cells to form distinct ganglia, but the larger nerve-cords are ganglionic throughout their extent. There are two pairs of longitudinal nerve-cords, united in front of the buccal mass by a supra-oesophageal or cerebral commissure. Ganglionic enlargements on this commissure are found only in *Callochiton doriae*.

The two ventral or pedal cords are united beneath the digestive tract by numerous transverse anastomoses. The two lateral or pallial cords are united posteriorly, dorsad of the anus, by a thick supra-rectal commissure (Fig. 31, VIII).

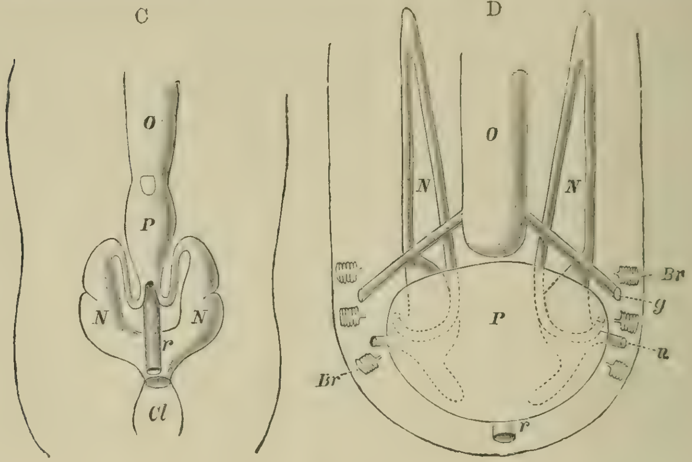

FIG. 30.

Diagrams of the excretory and reproductive organs of Amphineura. *C*, *Proneomenia*; *D*, *Chiton*. *Br*, ctenidia; *Cl*, cloacal or pallial chamber of *Proneomenia*; *g*, external aperture of the genital duct of *Chiton*; *N*, renal organ; *O*, gonad; *P*, pericardium; *r*, rectum; *u*, external aperture of renal organ of *Chiton*. (From Lankester, after Hubrecht.)

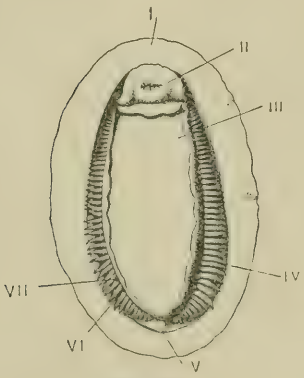

FIG. 30bis.

Ventral aspect of *Acanthopleura incana*. I, mantle; II, mouth; III, foot; IV, gills; V, anus; VI, right renal pore; VII, right genital pore (these two pores are better seen on the left-hand side of the body).

The cerebral commissure innervates the palps, the lips, and the muscles of the buccal bulb. Below the buccal bulb it is prolonged into an anterior labial commissure, which in turn gives rise to a stomato-gastric commissure: the last-named is to some extent ganglionic and has two branches, which unite with those of the opposite side on the upper and under side of the pharynx, and also with the infra-oesophageal subradular commissure. The subradular commissure supplies a pair of ganglia which are in close connection with a peculiar sense-organ lying on the floor of the mouth, in front of the radula. The labial and subradular commissures, together with the subradular organ, correspond to the homonomous parts in the Scaphoda and Cephalopoda.

The two great ventral or pedal cords give rise to the pedal nerves. The two great lateral or pallial cords chiefly send nerves to the mantle and the gills, and thus correspond to the whole of the pleural ganglia and the pallial nerves of the other Mollusca; a great part of the viscera (genital glands, kidneys, and heart) also receives nerves from these pallial cords.

The little differentiated head region bears no special sense-organ, except that the outer edges of the snout taper to form the labial palps. The lower wall of the buccal cavity is furnished with cyathiform gustatory bodies, whose nerves arise from the cerebral commissure; and, in front of the radula, there is the above-named "subradular organ," an epithelial projection, with nervous endings, lying on the two small subradular ganglia, and probably gustatory in function (Fig. 31, V).

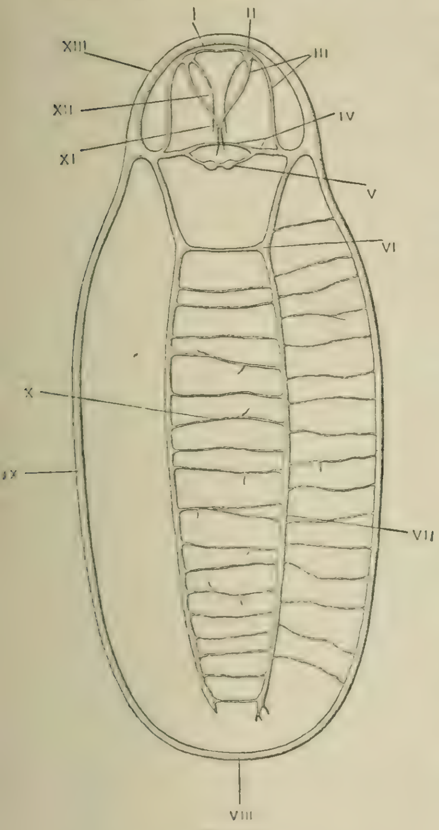

Fig. 31.

Nervous system of *Acanthochiton discrepans*, dorsal aspect. I, upper buccal commissure; II, upper buccal ganglion; III, stomato-gastric commissure; IV, labial commissure; V, subradular ganglia and commissure; VI, anterior (larger) pedal commissure; VII, pedal cord, with pallio-pedal anastomoses; VIII, supra-rectal pallial commissure; IX, pallial cord; X, pedal anastomosis; XI, stomato-gastric ganglia and radular nerves; XII, oesophageal nerves; XIII, cerebral commissure.

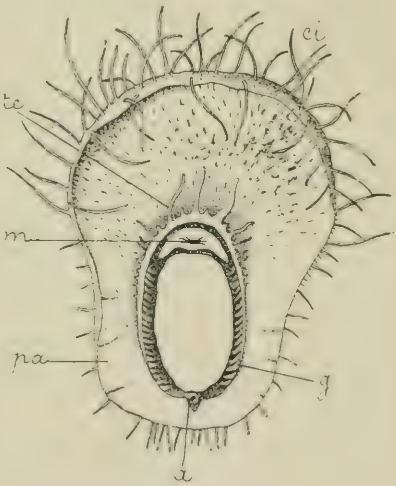

Fig. 32.

Placiphorella stimpsoni, ventral aspect; nearly natural size. *a*, anus; *ci*, pallial cirrhi; *g*, gills (between the two rows of gills is the oblong foot); *m*, mouth; *pa*, mantle; *te*, tentacles of the interior edge of the mantle. (After Plate.)

One osphradium is generally present on each side of the internal wall of the mantle, near the anus, more or less close to the last gill. In the Lepidopleuridae there are branchial sense-organs, related to accessory ganglia on the nerve of each gill (Burne). In *Placiphorella* the lower free margin of the mantle bears, in its anterior part, several long and thin appendages, which must be considered as sensory tentacles (Fig. 32).

Shell-Eyes.—The tegmentum of the shell-valves is traversed by peculiar pallial sense-organs in the form of epithelial papillae, containing nerve-endings covered with a cuticular hood. These organs are innervated from the pallial cords. According to their size, they are termed megalaesthetes or micraesthetes (Moseley). In various species of Chitonidae (and specially in exotic littoral forms of the sub-families Toniciinae and Liolophurinae), the megalaesthetes are converted into eyes, in which retina and pigment are always present. These eyes are frequently many thousands in number, and are most numerous on the anterior valve (Fig. 23, I). There are two kinds of such eyes: (1) Extra-pigmental eyes, with pigment in the tegmentum only, generally without a crystalline lens (except *Schizochiton incisus*); (2) intra-pigmental eyes, with pigment in the body of the aesthete, and always with a crystalline lens. The eyes are arranged in rows running diagonally from the median anterior beak of the valve to its external borders. There may be only one such row on either side, as in *Schizochiton*, or many such rows, as in *Tonicia*; and in *Acanthopleura*, in addition to the several diagonal rows, there are rows of eyes along the posterior margin of the valve, but these are not present in young specimens. In *Tonicia* the first pair of eyes is developed, at the close of larval life, on the second shell-valve. These organs are sensitive to disturbances in the water, and do not exist when the mucous projections of the mantle, referred to above, are present. Even those species of Chitons that are devoid of eyes are affected by light and shade: some littoral species, such as *Boreochiton cinereus*, do not move far from the light,

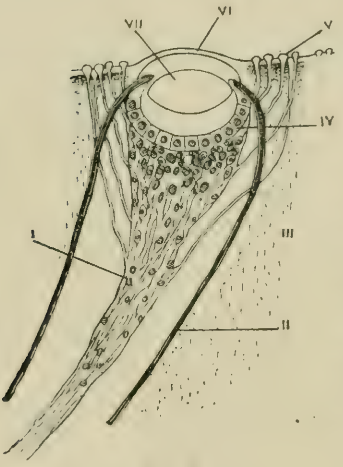

FIG. 33.

Axial section of a shell-eye of *Acanthopleura spiniger*. I, optic nerve with ganglionic cells; II, pigmented capsule of the eye; III, tegmentum of the shell; IV, rods of retina; V, micraesthetes; VI, calcareous cornea; VII, lens. (After Moseley.)

while others, such as *Ischnochiton magdalenensis*, are nocturnal in habit.

5. *Reproductive Organs.*—All the Polyplacophora are unisexual. The gonads are paired and symmetrical in *Nuttalochiton hyadesi*, but in all other species the gonad is single and median. It lies on the dorsal side of the body, between the aorta and intestine, and extends from the anterior end to the pericardium (Fig. 25, II). It is transversely wrinkled, and the ovary is frequently of a greenish, the testis of a red colour (*Chiton polii*, *Boreochiton cinereus*, etc.). In most species the ova are enclosed in a cellular follicle.

The paired genital ducts arise from near the posterior end of the gonad on the dorsal surface. Each duct is twice bent on itself, being directed first forwards, then backwards, and finally transversely toward the external opening. As a rule the gonaduct runs dorsad of the pallial nerve-cord, and its external opening is external to the cord, but in *Boreochiton ruber*, *B. marmoreus*, and *Katharina* it runs under the cord and opens internally to it. In the female the oviduct has a thick glandular investment (Fig. 25, III). The genital aperture is situated in front of the renal aperture, between two of the posterior gills. There may be from one (*Boreochiton*, *Lepidopleurus*, etc.) to nine (*Cryptoplax larvaeformis*: Fig. 26) gills between the genital and the renal apertures.

III. Embryology.

The eggs may be laid separately, in which case they are invested by a chitinous envelope frequently provided with spinous appendages; or, as in *Ischnochiton magdalenensis*, they may be laid in strings containing nearly 200,000 eggs (Fig. 34). These strings are not attached, and readily break into fragments. In many cases the ova are retained in the branchial furrow of the mother and undergo their development there (*Chiton polii*): in *Hemiarthrum setulosum* the embryos are protected in this manner until the eighth shell-valve is formed. In *Callistochiton viviparus* the ova are developed in the oviduct of the mother, and there is no larval stage.

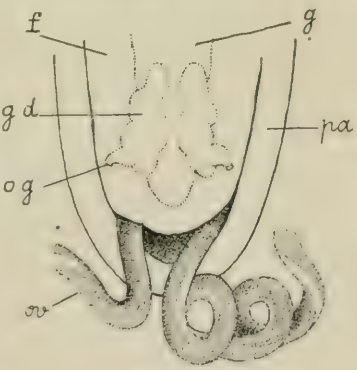

Fig. 34.

Ischnochiton magdalenensis, female, laying eggs, hind part, ventral aspect. *f*, foot; *g*, ovary; *g.d*, glandular oviduct; *o.g*, genital orifice; *ov*, ova; *pa*, mantle. (After Heath.)

The segmentation is total and, in the early stages, regular.

A gastrula is formed by invagination of the endodermic macromeres (Fig. 10, A). The orifice of invagination or blastopore is placed on the vegetative pole of the ovum, and does not close, but is gradually shifted towards the anterior end of the embryo. By the development of a ciliated ring or velum, in the centre of which there is an apical tuft of cilia, the embryo becomes a trochosphere larva (Fig. 14, A). The mesoderm arises from two endodermic cells, originally situated at the hinder side of the blastopore: they give origin to two bands of cells which extend right and left between the enteron and the ectoderm. In each band a cavity appears which becomes half of the coelom. The ectoderm around the blastopore is invaginated to form the oesophagus, a diverticulum of which becomes the radular caecum. At a late stage of development the intestine is placed in communication with the exterior by an anal invagination or proctodaeum. Anteriorly on the ventral or pedal surface a second ectodermic invagination forms the great pedal mucous gland, which is more or less atrophied at a later period. The gills appear as papillae much later than the anal invagination, the posterior one the first. The gonads originate by proliferation of the anterior wall of the pericardium.

The four great nerve-cords originate as four longitudinal and parallel ventral thickenings of the interior surface of the ectoderm, the two thickenings on each side of the body being closely approximated to one another at the time of their first appearance. At the extreme anterior end of each lateral or pallial cord and behind the velum is an eye, containing a closed cavity, or forming a simple epithelial ocellus. This eye disappears at a later stage, but in some species persists for a considerable length of time.

The shell-valves are formed as transverse thickenings of the dorsal cuticle behind the velum, the tegmentum being the first part of each valve to be laid down. The eight valves generally make their appearance simultaneously (*Chiton olivaceus*, *Ischnochiton magdalenensis*), but sometimes the eighth valve is formed later than the others (*Chiton polii*).

IV. Bionomics and Distribution.

The Polyplacophora are marine animals of sluggish habit, creeping slowly and for no great distance. They are generally herbivorous, and the majority of species live in the littoral zone, on rocks or under stones, but some inhabit the deeper regions of the sea, extending to a depth of more than 2100 fathoms (some *Lepidopleurus*, etc.). They can easily be kept in aquaria. Polyplacophora are distributed in all oceans and seas; more than three hundred living species have been recorded. They are fossil from the Ordovician.

V. Systematic Review of the Sub-Orders and Families of the Polyplacophora.

Sub-Order 1. Eoplacophora, Pilsbry.

Tegmentum coextensive with articulamentum, or the latter projecting in smooth, unslit plates.

Family 1. Lepidopleuridae, Pilsbry. Articulamentum without insertion plates or with unslit plates; terminal margins of end valves never elevated; form oval or oblong. Genera—*Lepidopleurus*, Risso (= *Leptochiton*, Gray) (Fig. 28, A). Without insertion plates, sutural laminae small; girdle minutely scaly or chaffy. *L. cancellatus*, Sow. North Atlantic and Mediterranean; various abyssal species. *Hanleya*, Gray. The anterior valve with an unslit insertion plate. *H. hanleyi*, Bean. North Atlantic. *Hemiarthrum*, Carpenter. Both anterior and posterior valves with smooth, unslit insertion plates; girdle downy. *Microplax*, Adams and Angas.

To this group belongs the extinct family of Gryptochitonidae, Pilsbry, together with various narrow and elongated Palaeozoic genera, whose one or two end valves have the terminal margins elevated.

Sub-Order 2. Mesoplacophora, Pilsbry.

Insertion plates well developed and slit.

Family 2. Ischnochitonidae, Dall. All the valves with slits, and the inner layer well covered by the outer. Sub-Family 1. Ischnochitoninae. No shell-eyes; sutural laminae separated; the slits in the valves 1 to 7 do not correspond with the ribs of the tegmentum. Genera—*Ischnochiton*, Gray. Smooth girdle. *Trachydermon*, Carpenter (with the sub-genera: *Tonicella*, Carpenter, and *Boreochiton*, Sars). Girdle, with small squamous spicula. *T. cinereus*, Linnaeus (Fig. 28, B) (= *T. marginatus*, Pennant). North Atlantic. *Chaetopleura*, Shuttleworth. Hairy girdle. *Stenoplax*, Carpenter. *Stenoradsia*, Carpenter. Sub-Family 2. Callochitoninae. With shell-eyes and united sutural laminae. Genus—*Callochiton*, Gray. *C. laevis*, Pennant. North Atlantic and Mediterranean. Sub-Family 3. Callistoplacinae. No shell-eyes; the slits in the valves 1 to 7 corresponding with the ribs of the tegmentum. Genera—*Callistochiton*, Carpenter (viviparous). *Nuttalochiton*, Plate.

Family 3. Mopaliidae, Dall. Each intermediate valve with a single slit; girdle hairy. Genera—*Mopalia*, Gray. *Placiphorella*, Carpenter (Fig. 32). *Placiphora*, Gray. *Placophoropsis*, Pilsbry.

Family 4. Acanthochitonidae, Pilsbry. Valves immersed in the girdle, and with small tegmentum. Genera—*Acanthochiton*, Leach (= *Cryptoconchus*, Guilding). Girdle with bundles of spicula. *A. fascicularis*, L. North Atlantic and Mediterranean. *Spongiochiton*, Carpenter. *Katharina*, Gray. *Amicula*, Gray. *Cryptochiton*, Middendorf. Valves quite concealed; no tegmentum. *C. stelleri*, Middendorf. Arctic.

Family 5. Cryptoplacidae, Dall. Vermiform, with thick girdle and small valves; insertion and sutural plates strongly drawn forward, sharp and smooth. Genera—*Cryptoplax*, Blainville (= *Chitonellus*, Lam.). Girdle without pores. *C. larvaeformis*, Blainville (Fig. 26). Eastern Archipelago. *Choneplax*, Carpenter. Girdle, with hair bundles within pores. *C. strigatus*, Sow.

SUB-ORDER 3. TELEOPLACOPHORA, Pilsbry.

All the valves, or at least the seven anterior, with insertion plates cut into teeth by slits.

FAMILY 6. CHITONIDAE, Guilding. Characters of the Sub-Order. SUB-FAMILY 1. CHITONINAE. No extra-pigmental eyes; insertion plates with pectinations between the fissures. Genera—*Chiton*, L. Squamous girdle. *Eudoxochiton*, Shuttleworth. Shaggy girdle. *Trachyodon*, Dall. *Radsia*, Gray. SUB-FAMILY 2. TONICIINAE. Extra-pigmentar shell eyes. Genera—*Tonicia*, Gray. Girdle smooth or shaggy (Fig. 23). *T. elegans*, Frembly. *Acanthopleura*, Gould. *Enoplochiton*, Gray. Squamous girdle. *E. niger*, Barnes. *Onithochiton*, Gray. *Schizochiton*, Gray. Spinous girdle; posterior valve notched. *S. incisus*, Sow. (Fig. 28, C). *Lorica*, Adams. *Loricella*, Pilsbry. *Liolophura*, Pilsbry.

ORDER 2. **Aplacophora**, von Jhering

(= *Solenogastres*, Gegenbaur = *Telobranchia*, Koren and Danielssen = *Scolecomorpha*, Lankester).

Our knowledge of the Aplacophora begins with Loven, who in 1841 described the genus *Chaetoderma*, and with Michael Sars, who mentions *Neomenia* in 1868, under the name *Solenopus*, but without description. *Chaetoderma* was for a long time believed to be a Gephyrean worm; and *Neomenia* was at first included among the Opisthobranchiate Gastropoda in a new Order, *Telobranchia*, by Koren and Danielssen.

Von Jhering was the first to point out the affinities of these two remarkable organisms with the Chitones, and to unite them in the new phylum Amphineura (1876); but he classed this phylum with the Vermes. Gegenbaur also classed the two genera *Chaetoderma* and *Neomenia* as worms under the name *Solenogastres*. But Hubrecht demonstrated the molluscan nature of the new genus *Proneomenia*, and its relationship to the Chitones. Lankester supported this view, and was followed by nearly all contemporary zoologists. It is generally believed that the Aplacophora are degenerate forms of Amphineura, derived from a chitonoid ancestor.

Definition.—The chief characteristics differentiating the Aplacophora from the Polyplacophora are the following: (1) they are worm-like in shape; (2) the body is completely invested by the mantle; (3) the mantle is devoid of a shell, but bears numerous calcified spicula over its whole surface; (4) the digestive tract is straight.

General Description.—The mantle covers the whole body, and is clothed by a rather thick cuticle, in which are implanted spicula (Fig. 35) developed from the tegumentary epithelium. The foot is nearly aborted or wanting. The nervous system consists of four great longitudinal trunks, with pedal and pedo-pallial anastomoses. The digestive tract is straight, the Aplacophora being carnivorous. The blood is red. The gonads are in open continuity with the fore part of the pericardium. The coelomo-ducts, corresponding to the renal sacs of the Polyplacophora, are gonaducts, and open externally into a posterior cloacal chamber, which serves as a rudimentary branchial cavity. There are two groups of Aplacophora: the Neomeniomorpha and the Chaetodermomorpha.

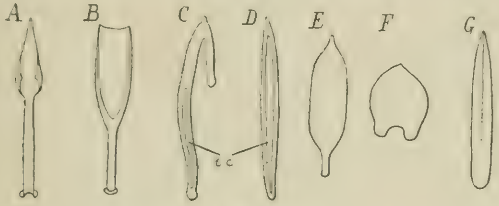

FIG. 35.

Spicules of various Aplacophora. *A*, *Neomenia* (Wiren); *B*, *Dondersia* (Hubrecht); *C*, *Paramenia* (Pruvot); *D*, *Proneomenia*; *E*, *Stylomenia* (Pruvot); *F*, *Myzomenia* (Pruvot); *G*, *Chaetoderma* (Wiren). *i.c*, internal cavity.

SUB-ORDER 1. NEOMENIOMORPHA.

Aplacophora with a distinct longitudinal ventral groove; bisexual, with paired genital glands and without differentiated liver.

I. EXTERNAL CHARACTERS.

The mantle extends over the sides of the body so as to cover the greater part of the ventral surface, leaving only a narrow median longitudinal furrow uncovered. The pallial cuticle, which is very thick in some species, contains a number of long, hollow, calcified, acicular, or flattened spicules (Fig. 35) borne on epithelial papillae. In some cases, when it is very thick, the cuticle also includes sensory papillae. A small longitudinal projection in the ventral furrow is the vestige of the foot. The antero-ventral region of the body is occupied by a large mucous gland, whose secretion is poured into a ciliated pit in the anterior part of the ventral furrow, the whole structure corresponding to the embryonic pedal gland of some Chitones. Smaller mucous glands are also found along the pedal projection. Posteriorly there is a terminal cloacal or branchial cavity, into which opens a thick mucous gland, situated between the foot and anus.

II. ANATOMY.

Digestive Tract.—The mouth is anterior and ventral, and is frequently surrounded by papillae, probably sensory in function. It opens into a muscular and sometimes protractile pharynx lined by a thick cuticle. The salivary glands and radular sac open into the pharynx. The radula (Fig. 36), when present, comprises several rows of teeth, and may be (1) polystichous, with a continuous line of teeth in each row (*Proneomenia* and *Macellomenia*), in which case a basal membrane may be present, forming a true continuous polyserial radula (*Proneomenia acuminata*, *P. sluiteri*, *P. gerlachei*), or absent, forming a discontinuous polyserial radula (*P. vagans*); (2) distichous, with two separate teeth (*Paramenia*, *Pararhopalia*, *Ismenia*, *Lepidomenia*, *Dinomenia*); (3) monostichous, with a single tooth (*Stylomenia*, *Dondersia*, *Amphimenia*, *Proparamenia*). The radula is entirely absent in the Neomeniidae, in *Rhopalomenia*, *Pruvotia*, *Strophomenia*, and *Notomenia*.

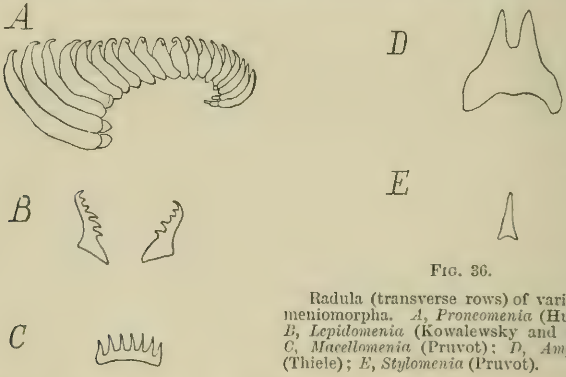

FIG. 36.

Radula (transverse rows) of various Neomeniomorpha. *A*, *Proneomenia* (Hubrecht); *B*, *Lepidomenia* (Kowalewsky and Marion); *C*, *Macellomenia* (Pruvot); *D*, *Amphimenia* (Thiele); *E*, *Stylomenia* (Pruvot).

The salivary glands form a symmetrical pair, lying on the ventral side, and opening on a subradular prominence; their ducts sometimes unite before opening into the pharynx. They correspond to the subradular glands of the Polyplacophora and the posterior salivary glands of the Cephalopoda. In some forms there is a second pair of salivary glands, dorsal or dorso-lateral in position, opening by a single duct into the mid-pharynx (*Paramenia*, some species of *Proneomenia*: Fig. 37, *gl.s.d*). Several genera, among them *Neomenia*, are devoid of salivary glands. The oesophagus is generally short, and leads into a cylindrical and rectilinear stomach, which frequently sends forward a caecum dorsad of the oesophagus, and is provided with symmetrical lateral caeca, giving to the organ the appearance of regular segmentation. The whole surface of the stomach is lined by a secretory, or so-called hepatic epithelium, and its dorsal wall is ciliated. The intestine is straight and short, with thin walls lined by a ciliated epithelium. The anus opens into the branchial or cloacal chamber, together with the kidneys and sometimes the anal mucous gland (Fig. 38).

Circulatory System. — There are no true blood-vessels with definite walls, but there are two well-marked blood-spaces — a ventral sinus between the foot and digestive tract, and a dorsal tubular sinus or aorta whose hinder part forms a contractile heart. The heart is enclosed in the pericardium and is fastened to its dorsal wall, except in *Neomenia*, where it is free. The blood is red owing to the presence of haemoglobin in the rounded or ovate blood-corpuscles.

In the Neomeniidae and most of the Parameniidae there is a more or less extensive circlet of gills on the inner walls of the cloacal chamber. These gills are epithelial folds or laminae, whose cavities communicate freely with the haemocoele and the above-mentioned sinuses. In the species in which no gills are present the venous blood of the ventral sinus is oxygenated through the epithelium of the inner wall of the cloacal chamber and the surface of the foot. Where gills are present the blood passes into them and is returned to the heart by two auricular ducts in *Neomenia*.

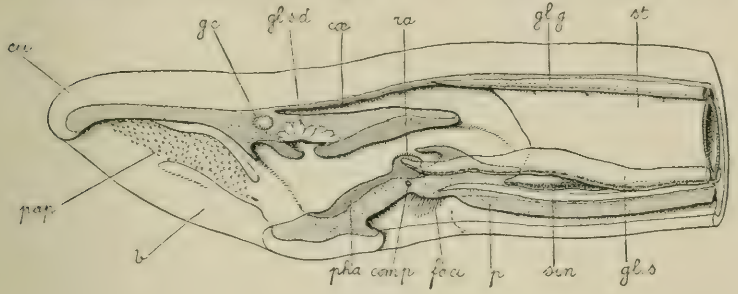

FIG. 37.

Proneomenia gerlachei, right half of the anterior part of the body; left-side view. *b*, mouth; *cae*, pharyngeal caecum; *com.p*, pedal commissure; *cu*, cuticula; *fo.ci*, ciliated fossa; *g.c*, cerebral ganglion; *gl.g*, gonad; *gl.s*, salivary gland; *gl.s.d*, dorsal salivary gland; *p*, foot; *pap*, buccal papillae; *pha*, pharynx; *ra*, radula; *sin*, ventral sinus; *st*, stomach.

Excretory Organs. — The pericardium occupies the posterior region of the body dorsad of the rectum. The dorsal and lateral parts of its inner wall are ciliated, and its cavity communicates with the exterior by means of a pair of renal ducts, which open into the cloacal chamber below the anus. In *Strophomenia* the renal orifices are adjacent, but separate from one another as in *Chaetoderma*, but in all other Neomeniomorpha the renal ducts open into the cloaca by a common aperture (Fig. 30, C). As in the Polyplacophora, the renal tubes are first directed forwards and then turn sharply backwards to run parallel to their former course. But the kidneys of Neomeniomorpha are very different both in structure and conformation from those of the Polyplacophora ; they serve also as efferent ducts for the genital products, and their inner walls—particularly the conjoined terminal pouch—are very glandular, and form an organ which secretes the egg-shell. Moreover (except in *Lepidomenia*, in which they are very simple) they bear one or two pairs of caecal appendages on the proximal part of their course, the caeca nearer to the pericardium serving as sperm reservoirs.

Nervous System.—On the dorsal side, and in front of the buccal bulb, there is a large supra-oesophageal nerve-mass, formed by two conjoined ganglia, and often provided with accessory lobes. Two ganglionated nerve-trunks are given off from each side of this cerebral ganglion ; that on the dorsal side being the pleural, that on the ventral side the pedal cord. The two cords may originate separately from the cerebral ganglion, or may be fused at their origin and diverge after entering a pleural ganglion (*Neomenia*). They correspond to the homonomous cords in the Polyplacophora. The pedal cords enlarge to form a pair of pedal ganglia, united by a thick pedal commissure, and are continued posteriorly as two regularly varicose trunks united by transverse anastomoses. The two pallial cords are joined together posteriorly by a supra-rectal commissure, which is double in *Proneomenia sluiteri*, but absent in *Dinomenia verrucosa* and *Rhopalomenia indica*. An ovoid ganglion is generally borne on the supra-rectal commissure. The pallial cord of either side is united to the corresponding pedal cord by more or less numerous anastomoses. In some forms, *e.g. Paramenia*, the pedal cords are united to the pallial some way in front of the supra-rectal commissure. A small anterior infra-oesophageal or stomato-

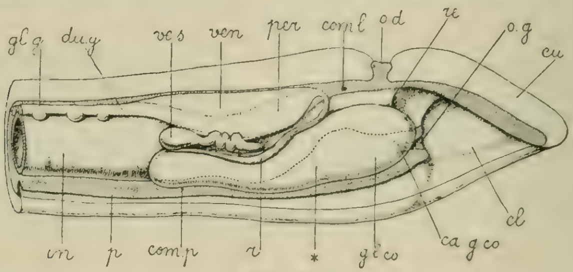

Fig. 38.

Proneomenia gerlachei, right half of the posterior part of the body, left-side view. *ca.g.co*, common median cavity of the two shell-glands ; *cl*, cloaca ; *com.l*, supra-rectal pallial commissure ; *com.p*, the most posterior pedal commissure ; *cu*, cuticula ; *du.g*, opening of the gonad in the pericardium ; *gl.co*, shell-gland of the left kidney ; *gl.g*, left gonad ; *in*, intestine ; *o.d*, dorsal sense-organ ; *o.g*, common opening of the two reno-genital ducts ; *p*, foot ; *per*, pericardium ; *r*, left kidney ; *re*, rectum ; *ven*, ventricle of heart ; *ve.s*, seminal vesicle : * anterior limit of the junction of the two shell-glands.

gastric commissure is given off from the cerebral mass, and enters a pair of small ganglia situated in the median line between the oesophagus and the radular sac; moreover, the two same upper buccal and subradular commissures as in the Chitones are present, at least in *Proneomenia* and *Rhopalomenia* (Heath).

The only organs of special sense are the club-shaped epithelial papillae in the thickened cuticle of the Proneomeniidae, *Neomenia*, and the following Parameniidae, *Dinomenia*, *Proparamenia*, and *Paramenia*. There is also a median invaginable sensory papilla situated on the dorsal posterior surface, above the rectum. It is not covered by the cuticle, and may be multiple, as in *Dondersia*, or absent, as in *Hemimenia* and perhaps *Strophomenia*.

Generative Organs.—The Neomeniomorpha are hermaphrodite. The gonads are paired tubular structures, separately opening posteriorly into the pericardium (Fig. 30, C) and extending forward close under the dorsal sinus to near the front end of the body. The ova are developed on the median, the spermatozoa on the outer wall of each gonad. The sexual products pass into the pericardium, whence they are driven by the pericardial cilia into the kidneys, which, as has been explained above, serve as gonaducts and are provided with receptacula seminis and shell-glands. In several species paired excitatory organs, in the form of protrusible calcareous spicules, are situated in the cloacal chamber on either side of the uro-genital orifice.

III. EMBRYOLOGY.

Little is known of the development of the group. The ova are laid separately. In *Myzomenia banyulensis* (Pruvot) the segmentation is regular, and an invaginate gastrula with an originally posterior blastopore is formed. An anterior ciliated ring or velum is formed, having in its middle a tuft of cilia, which is eventually transformed into a single terminal flagellum (Fig. 17). The external surface of the trochophore larva thus formed is made up of a number of ciliated test-cells, which—as in the Lamellibranchiate *Yoldia*—eventually are cast off and the mantle is formed beneath. The post-velar region of the embryo elongates, and its ectoderm cells develop spicules. Finally, the velum disappears, and seven imbricated calcareous plates, made up of more or less flattened, closely-apposed spicules, are formed on the dorsal surface (Fig. 39).

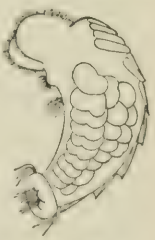

Fig. 39.

An advanced larva of *Myzomenia banyulensis*, the seventh day after the test has fallen off. (After Pruvot.)

IV. BIONOMICS.

The Neomeniomorpha are marine animals, living in depths of from 15 to 800 fathoms, but are most abundant in 50 fathoms. They inhabit oozy bottoms, and are found crawling on corals and hydroid zoophytes, on which they feed. They have been found in nearly all seas except the S.E. and N.W. Pacific and the S. Atlantic. The British genera are *Neomenia*, *Rhopalomenia*, and *Myzomenia*. About forty species, included in twenty genera, have been recorded up to the present time.

V. SYSTEMATIC REVIEW OF THE NEOMENIOMORPHA.

FAMILY 1. LEPIDOMENIIDAE, Pruvot. Slender, tapering behind, with subventral cloacal orifice ; thin cuticle without papillae ; flattened spicules ; no gills. Genera—*Lepidomenia*, Kowalewsky and Marion. *Ismenia*, Pruvot. *Ichthyodes*, Pruvot. *Stylomenia*, Pruvot. *Dondersia*, Hubrecht. *Nematomenia*, Simroth. *Myzomenia*, Simroth. *M. banyulensis*, Pruvot. Mediterranean and Plymouth.

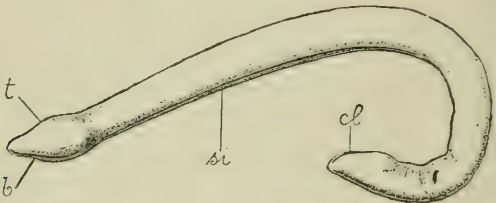

FIG. 40.

Proneomenia gerlachei, left-side view. *b*, mouth ; *cl*, cloaca ; *si*, foot-groove ; *t*, head.

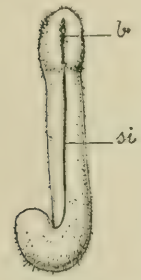

FIG. 41.

Paramenia cryophila, ventral aspect. *b*, mouth ; *si*, foot-groove.

FAMILY 2. NEOMENIIDAE, von Jhering. Short, truncated in front and behind ; cloacal orifice transverse ; gills present ; rather thin cuticle ; no radula. Genera—*Neomenia*, Tullberg. *N. carinata*, Tullberg. North Atlantic, N. and N.W. Scotland. *Hemimenia*, Nierstrasz.

FAMILY 3. PRONEOMENIIDAE, Pruvot. Elongated, cylindrical, rounded at both ends ; thick cuticle with acicular spicules ; radula polystichous or wanting. Genera — *Proneomenia*, Hubrecht (Fig. 40). *Amphimenia*, Thiele. *Echinomenia*, Simroth. *Rhopalomenia*, Simroth. *R. aglaopheniae*. Mediterranean and Plymouth. *Notomenia*, Thiele. *Pruvotia*, Thiele. *Strophomenia*, Pruvot.

FAMILY 4. PARAMENIIDAE, Pruvot. Short, and truncated in front ; thick cuticle (often without papillae) ; gills and radula present. Genera—*Paramenia*, Pruvot (Fig. 41). *Macellomenia*, Simroth. *Pararhopalia*, Simroth. *Dinomenia*, Nierstrasz. *Cyclomenia*, Nierstrasz. *Proparamenia*, Nierstrasz, *Uncimenia*, Nierstrasz. *Kruppomenia*, Nierstrasz.

SUB-ORDER 2. CHAETODERMOMORPHA.

Aplacophora without distinct longitudinal ventral (or pedal) groove, with unpaired unisexual gonad, with differentiated liver, and with posterior cloacal chamber provided with two bipectinate gills.

Anatomy.—The mantle covers the whole surface of the body, which is therefore cylindrical and vermiform in appearance. The hinder half of the body is a little stouter than the anterior; the posterior extremity swollen and bell-shaped, forming the widely cloacal chamber. The whole body has a uniform covering of short, compressed, calcareous spicules implanted in the cuticula.

The mouth is anterior, terminal, and crescentic, owing to the presence of a rounded ventral shield. *Chaetoderma radulifera* alone is provided with mandibles. The buccal cavity, whose anterior part is partially protrusible, bears on its floor a very peculiar radula, which may consist of (*a*) a single large tooth (Fig. 43, C), upon which two small teeth are placed (*C. nitidulum* and *C. productum*); (*b*) a single large tooth, upon which is a row of teeth (*C. gutturosum*; (*c*) no large tooth, several rows of three teeth one behind the other (*C. radulifera*); (*d*) several distichous rows of two teeth each (*C. challengeri*). Two pairs of salivary glands, similar to those in the Neomeniomorpha, open into the buccal cavity. The digestive tract is quite straight, and narrows towards the middle of its course to form the intestine. Just before it narrows it receives the duct of a more or less extensive hepatic caecum, which extends backwards on the ventral side of the intestine. The hepatic caecum, large in most species, is feebly developed in *C. challengeri*. The anus opens in the median line in the cloacal chamber (Fig. 43, B).

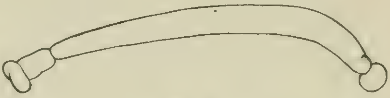

FIG. 42.

Chaetoderma nitidulum, Loven. The cephalic enlargement is to the left, the cloacal or pallial chamber (containing the concealed pair of ctenidia) to the right. (From Lankester, after Graff.)

The heart is posterior and dorsal, and lies nearly free in the pericardial cavity. It is traversed by the retractor muscles of the gills. In its main features the circulatory system resembles that of the Neomeniomorpha. The posterior extremity of the body is hollowed to form a bell-shaped cloacal cavity, which has a contractile aperture and contains a pair of large branchiae placed symmetrically right and left of the anus. Each branchia bears a double row of branchial plates, as is the case in the Polyplacophora (Fig 43, B).

The two renal ducts are more evidently true excretory organs than in the Neomeniomorpha. They originate from the posterior corners of the pericardial cavity, run forward under the floor of the pericardium, and then turn outwards and backwards to run back to their respective apertures right and left of the anus. Their thin walls are lined by a ciliated epithelium, and there are no accessory generative organs.

In the nervous system there are two intimately fused cerebral

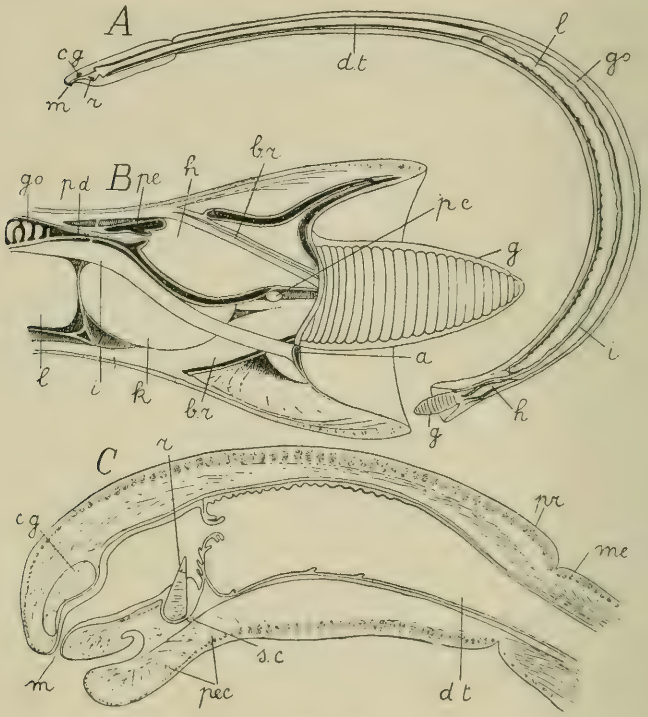

Fig. 43.

Chaetoderma nitidulum. *A*, median sagittal section; *B*, sagittal section of the posterior extremity; *C*, sagittal section of the anterior extremity. *a*, anus; *br*, retractor muscle of the branchiae; *c.g*, cerebral ganglion; *d.t*, digestive tract; *g*, gill; *go*, gonad; *h*, heart; *i*, intestine; *k*, kidney; *l*, liver; *m*, mouth; *me*, "mesothorax"; *p.c*, pallial suprarectal commissure; *p.d*, pericardial duct; *pe*, pericardium; *pe.c*, pedal commissures; *pr*, "prothorax"; *r*, radula; *s.c*, sublingual commissure. (After Wiren.)

ganglia bearing accessory lobes. Each ganglion gives rise to two longitudinal nerve-cords, the ventral or pedal cord being more slender than the dorsal or pallial cord. In the anterior part of their course the pedal and pallial cords of either side run parallel and adjacent to one another, but in the posterior region of the body they are fused together, as in *Paramenia*, and the two palliopedal cords thus formed are united dorsad of the rectum by a ganglionic swelling. A small perirectal commissure originates from this swelling. The pedal cords are united with one another and with the pallial cords of the same side by anastomoses in the anterior region of the body. A small stomato-gastric commissure, bearing two small stomato-gastric ganglia on the middle of its course, arises from the cerebral ganglia and surrounds the oesophagus. There are no organs of special sense except a dorsal posterior and median pit, corresponding to the precloacal fossa of the Neomeniomorpha.

The sexes are separate. The azygos gonad occupies the same position as the paired gonads of the Neomeniomorpha, and communicates by a median aperture with the pericardial cavity. The generative products are conducted from the pericardium to the exterior by the renal ducts. The embryology of the group is quite unknown.

The Chaetodermomorpha are marine animals feeding on lowly-organised forms of life, such as Protozoa, etc. They are found in oozy bottoms from a depth of 15 fathoms to abyssal regions. The nine recorded species of the single genus *Chaetoderma* come from the North Atlantic, North Pacific, and Arctic Oceans, the Sea of Marmora, the Eastern Archipelago, and the Philippine Islands.

Family CHAETODERMATIDAE, von Jhering. Genus—*Chaetoderma*, Loven. The characters are those of the sub-order. *Limifossor*, Heath (Alaska).

PHYLOGENY OF THE AMPHINEURA.

The Polyplacophora present the most archaic characters among the Amphineura. The Aplacophora, on the other hand, are specialised in the following respects: (1) in the great reduction of the foot; (2) the disappearance of the shell (*Cryptoplax*, among the Polyplacophora, shows how these two reductions may take place simultaneously); (3) the absence of the radula in several forms. The Chaetodermomorpha seem to be more specialised in these points than the Neomeniomorpha.

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CHAPTER III

THE GASTROPODA

CLASS II.—GASTROPODA, CUVIER

(= PARACEPHALOPHORA, Blainville; ANISOPLEURA, Lankester).

Sub-Class I. Streptoneura.
  - Order 1. **Aspidobranchia.**
    - Sub-Order 1. **Docoglossa.**
    - ,, 2. **Rhipidoglossa.**
  - Order 2. **Pectinibranchia.**
    - Sub-Order 1. **Taenioglossa.**
    - ,, 2. **Stenoglossa.**

Sub-Class II. Euthyneura.
  - Order 1. **Opisthobranchia.**
    - Sub-Order 1. **Tectibranchia.**
    - ,, 2. **Nudibranchia.**
  - Order 2. **Pulmonata.**
    - Sub-Order 1. **Basommatophora.**
    - ,, 2. **Stylommatophora.**

Definition.—The Gastropoda, together with the Scaphopoda and the Lamellibranchia, form the branch Prorhipidoglossomorpha of the Mollusca, that is to say, a group in which the gonads are no longer in direct communication with the pericardium, the foot is wholly posterior to the head, and a visceral commissure is present. The Gastropods are a class of the Prorhipidoglossomorpha specially characterised, firstly, by their asymmetrical organisation; secondly, by their well-developed head; and thirdly, by their shell, which is formed of one piece and coiled in a spiral, at least in the larval stage.

I. General Description and External Characters.

The three external divisions of the body, head, foot, and mantle are well defined. The head is well developed, and forms a more or less cylindrical mass, but is sometimes flattened. At its anterior extremity is the mouth, and dorsally it bears one or two pairs of tentacles. There is one pair of tentacles in the Streptoneura (Fig. 44), the "Thecosomata" (Fig. 63), in *Phyllirhoë* (Fig. 161), *Thecacera*, the Proctonotidae, the Elysiidae (Fig. 170), the basommatophorous Pulmonates, and *Janella* (Fig. 178). There are two pairs in the majority of Opisthobranchs (Fig. 154) and in the stylommatophorous Pulmonates (Fig. 172). The tentacles either are or bear sensory organs; they are contractile, and in the Stylommatophora invaginable. The right tentacle of both sexes bears an appendage in *Bathysciadium* (Fig. 126), certain Trochidae (Fig. 130), and *Calyptraea*. The form of the tentacles varies greatly in different groups. Sometimes they are atrophied, and they may even disappear without leaving a trace, as in *Olivella*, *Homalogyra*, certain species of *Terebra*, *Pterotrachea* (Fig. 143), *Limapontia*, and *Pseudovermis* (Fig. 169). In the majority of the Bullidae the two pairs of tentacles are enlarged and transformed into a quadrangular shield (Fig. 148), the four corners of which correspond to the tips of the four tentacles. The single pair, much reduced in certain Basommatophora (Amphibolidae, Otinidae, Fig. 173, Siphonariidae), similarly gives rise to the appearance of a flattened disc on the top of the head. The anterior pair of tentacles in the Pleurobranchidae (Fig. 157) and in various Nudibranchs (Tritoniidae, Fig. 83, Dendronotidae, Tethyidae, etc.) is transformed into a more or less well-developed frontal veil. Finally, the tentacles are flattened (*Narica*); split (Pyramidellidae, Fig. 137, *Solarium*, the posterior pair in many Opisthobranchs); bifurcate (*Janthina*, certain Elysiomorpha); or multifid (the posterior pair in many Nudibranchs, *Dendronotus*, *Ancula*, Fig. 163). In some species, on either side of the buccal orifice, there is another pair of appendages of greater or less length, known as the labial palps. These are found in *Trochus infundibulum*, *Ampullaria*, *Jeffreysia*, *Choristes*, among the Streptoneura; and among the Euthyneura in sundry Pulmonates (*Glandina*, *Limnaea*, in which they form a sort of buccal veil, Fig. 107), and in Tectibranchs. In addition to the above-mentioned cephalic appendages of the adult, the following structures should be noted: the cephalic or frontal lobes, situated between the two tentacles and consisting of projections of various shape, in many Rhipidoglossa and in *Fossarus*; the dorsal median crest in *Olivella* and *Janus*; and finally, the pseudopallium, an expansion of the cephalic integument surrounding the whole shell, with the exception of the summit of the spire, in *Stylifer* and allied parasitic forms (Fig. 20).

1. *The Foot.*—This is primitively and normally formed by a powerful mass of ventral muscles with a more or less elongated

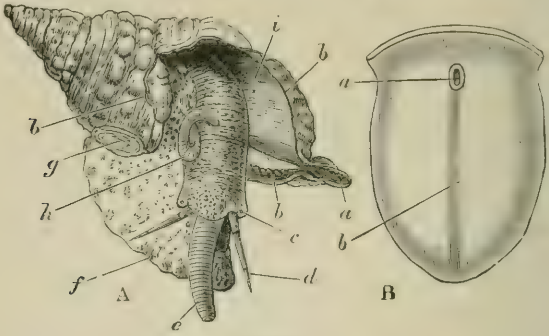


FIG. 44.

A, *Triton variegatum*, animal and shell, seen from the right side. *a*, siphonal notch of the shell occupied by the siphonal fold of the mantle-skirt; *b*, edge of the mantle-skirt resting on the shell; *c*, cephalic eye; *d*, cephalic tentacle; *e*, proboscis or buccal introvert in a state of eversion; *f*, foot; *g*, operculum; *h*, penis; *i*, under-surface of the mantle-skirt, forming the roof of the sub-pallial chamber. (From Lankester, after Poli.) *B*, sole of the foot of *Hemifusus tuba*, to show, *a*, the pore of a pedal gland; *b*, median line of the foot. (From Lankester, after Souleyet.)

ventral creeping surface (Fig. 44, B). But this primitive condition may be modified in relation to different conditions of existence. Thus, among sedentary Gastropods the foot is reduced to a simple discoidal prominence in such fixed forms as *Vermetus* (Fig. 45) and

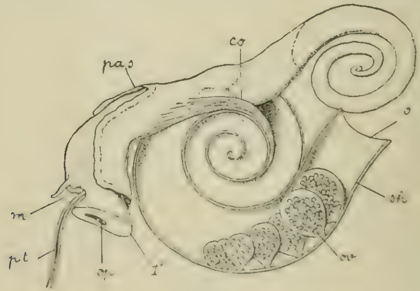


FIG. 45.

Vermetus triqueter, with broken shell; left-side view. *co*, columellar muscle; *f*, foot; *m*, mouth; *o*, aperture of the shell; *op*, operculum; *ov*, eggs; *pa.s*, mantle slit; *p.t*, pedal tentacles; *sh*, shell. (After Lacaze-Duthiers.)

Magilus. In *Bathysciadium* (Fig. 126) the ventral surface of the foot assumes the form of a sucker, the central portion of which is covered by a thick cuticle, and the circumference is ciliated. In the parasitic forms *Stylifer* and *Thyca* the foot is atrophied and is represented only by a small ventral appendage. Among the free-swimming Gastropods we find that in the Heteropods the foot is laterally compressed to form a vertical natatory lobe held uppermost in swimming (Fig. 142), but in *Phyllirhoë* it no longer exists as a differentiated organ (Fig. 161). In leaping Gastropods, such as *Rostellaria* among the Strombidae (Fig. 46), the foot is also laterally compressed, and its ventral surface, if not displaced anteriorly, is not flat. In *Harpa* the posterior part of the foot may be cast off by a process of autotomy.

The creeping sole is often divided by a median longitudinal furrow: this may be seen in sundry Rhipidoglossa, *e.g.* *Trochus*, *Stomatella*, *Phasianella*; and in Taenioglossa such as *Littorina* and *Cyclostoma*: in the last-named genus the two halves of the foot contract alternately during progression. A transverse furrow, crossing the anterior half of the foot, is found in the Olividae, *Pomatiopsis*, many Auriculidae, *Otina*, and *Cyerce*.

Certain parts of the foot may exhibit special differentiations. (1) Its two anterior angles are prolonged into tentacles in *Cyclostrema*, *Valvata* (Fig. 132), *Choristes*, *Olivella*, *Eolis*, etc. (2) The anterior margin of the foot may be furnished with a number of small tactile papillae as in *Trochus*, etc., or there may be a small fleshy projection, called the mentum, between it and the mouth, below the aperture of the supra-pedal gland, as in the Pyramidellidae (Fig. 137), *Siliquaria*, *Aclis*, *Vermetus*. In *Capulus* there is a little projecting tongue-shaped structure above the anterior margin of the foot and below the snout, and in *Vermetus* two symmetrical tentacles are present in the same position, on either side of the aperture of the supra-pedal gland. (3) In various fossorial Gastropods the whole anterior region of the foot is somewhat elevated above the head, to form the propodium. This region is distinctly separated from the rest of the foot by a constriction in the Harpidae and by a transverse furrow in the Olividae. The propodium is particularly well developed in the Naticidae, in which it is reflected over the whole cephalic region to form a powerful digging organ (Fig. 47). (4) The lateral margins of the foot are expanded to form fins or parapodia in certain Olividae, and particularly in a number of Opisthobranchs, as, for example, in *Gastropteron*, *Acera*, etc.; among the Bullidae, the Pteropods, *Aplysia*, etc. In *Notarchus* these two lobes are united above the body in such a manner as to form a muscular sac open in front, but closed behind and at the sides. By forcibly expelling water through the anterior aperture, the animal makes use of the sac as an organ of locomotion. (5) The posterior region of the foot is often separated off as a distinct operculigerous lobe, as may be seen in the Strombidae (Fig. 46), *Xenophorus* (Fig. 134), and the Atlantidae (Fig. 141). In some Marginellidae there is a posterior dorsal discoid lobe. In *Nassa* and in allied forms the posterior extremity of the foot bears a pair of tentacles which are sometimes bifurcated, and in *Phos* there is a single filament in this position. In *Pterotrachea* the foot terminates posteriorly in a long filiform contractile appendage, bearing several annular varicosities. In *Cymbulia* the posterior lobe of the foot also ends in a long whip-like appendage. (6) On the sides of the foot, at about the middle of its height, there is often a ridge, the epipodium, extending from the head to the posterior end of the foot. This ridge is specially well developed in various Rhipidoglossa (Fig. 130, VIII), and may bear appendages of greater or less length, sensory organs, and pigment spots, the last-named, however, showing no trace of the structure of eyes. The anterior part of the epipodium generally forms a cervical lobe, which exhibits a characteristic asymmetry in certain Trochidae. The epipodium is found also in *Litiopa*, the Rissoidae, *Narica*, *Janthina*, etc., and a portion of it is represented by the cervical lobes in *Paludina*, *Ampullaria*, and *Calyptraea*.

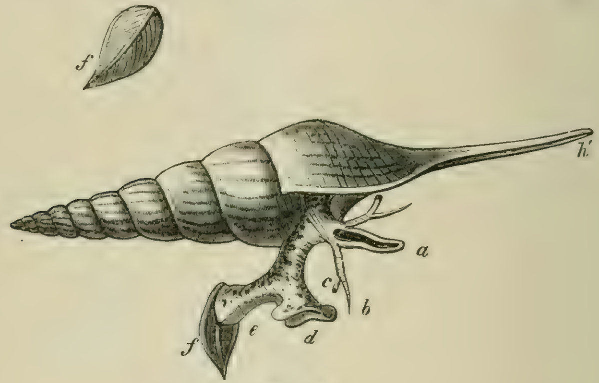


Fig. 46.

Rostellaria rectirostris, animal and shell, right-side view. *a*, snout or rostrum; *b*, cephalic tentacle; *c*, eye; *d*, anterior part of the foot; *e*, posterior (operculigerous) part of the foot; *f*, operculum; *h'*, anterior canal of the shell, occupied by the pallial siphon. (From Lankester, after Adams.)

The surface of the foot is normally furnished with a large number of unicellular mucous glands, and very often these cells are specially accumulated in invaginations of the integument, distinguished as pedal glands. The most important of these invaginations are—(1) The anterior groove of the foot (Fig. 144, IV), into which open the so-called labial glands: it is often continued into a fairly long canal. This anterior pedal gland is very generally present in the aquatic creeping species of Streptoneura and Opisthobranchs; it secretes the mucus which lubricates the surface of the foot, and is auxiliary to creeping whether it be on the bottom of the sea or on the surface in a reversed position. (2) The supra-pedal gland opens in the middle line between the snout and the anterior border of the foot. It is most commonly found in sessile Streptoneura (*Vermetus*, *Hipponyx*) and in terrestrial forms such as *Cyclostoma* and the Pulmonata. It is often very deep, and extends for nearly the whole length of the foot: its walls are thrown into folds and are ciliated ventrally in the majority of the Pulmonates. (3) The ventral pedal pore, situated in the middle line in the anterior moiety of the foot, is the aperture of a more or less extensive and often ramified cavity into which the glands of the sole or the pedal glands properly so called pour their secretion (Figs. 44, B; 144, I). This organ is comparable with the byssogenous gland of Lamellibranchs (Fig. 197), and is found in the following genera: in *Cyclostoma*, in which it is composed of multiple tubules; in *Cypraea*, *Hemifusus* (Fig. 44), *Cassis*, and a large number of Rachiglossa and Toxiglossa, viz. in the Fasciolariidae, Turbinellidae, *Nassa*, *Murex*, the Olividae, Marginellidae, and Conidae (Fig. 144). Its opening was formerly mistaken for an aquiferous pore. (4) The posterior mucous glands may be either dorsal or ventral in position. The former are characteristic of terrestrial Gastropods, such as the Pulmonates and certain Cyclostomatidae, in which they are often surmounted by a simple or multiple horn-shaped protuberance (*Orpiella*, *Plectrophorus*, *Dermatocera*). The ventral posterior glands are simple localisations of the dermic glands, and occur in various Opisthobranchs; they are not sensibly invaginated in the Pleurobranchidae and Pleurophyllidae, but are invaginated and form a long canal in *Gastropteron*. The product of secretion of the pedal glands in many cases solidifies on contact with the air or water and serves for the suspension of the animal. In some species of *Limax*, *Litiopa*, *Cerithidea*, etc., it assumes a filamentous form; and in both sexes of *Janthina*, whether viviparous or not, it is filled with air-bubbles and forms a float, covering the ventral surface of the foot, beneath which the animal is suspended (Fig. 135).

The ventral border of the flattened and fin-like mesopodium of the Heteropoda exhibits, in the male at any rate, an invagination in the form of a sucker (Figs. 141, 142, *d'*). A similar sucker exists on the ventral or pedal area of some species of *Phyllirhoë*, but in no Gastropod does the foot exhibit an aquiferous pore, in the sense formerly attached to this term. In some forms, however, and at all events in the Naticidae, there is a system of aquiferous spaces in the foot; these spaces are completely separated from the circulatory apparatus and serve to distend the foot (Fig. 47, VIII) in the action of burrowing in the sand or mud.

The foot often bears on its posterior dorsal aspect a solid sclerite, known as the operculum, which, on the retraction of the animal, serves to close the aperture of the shell. The operculum is sometimes borne on a differentiated portion of the foot as in *Xenophorus* (Fig. 134), *Pterocera* (Fig. 75), *Atlanta* (Fig. 141), or on a distinct expansion, which in *Natica* is reflected over a portion of the shell. An operculum is present in almost all adult Streptoneura, the exceptions being the Docoglossa, the Fissurellidae, the Haliotidae, *Gena*, *Stomatia*, the Proserpinidae, Calyptraeidae, Capulidae, Hipponycidae, Cypraeidae, Doliidae, Marginellidae, Harpidae, the majority of the Mitridae, many Cancellariidae and Conidae, *Oliva*, the Janthinidae, etc. But in all these cases, with the exception of the larva of *Stylifer*, an operculum is present during development, as may be seen, for example, in the Patellidae, *Fissurella*, *Calyptraea*, *Janthina*, *Carinaria*, etc. The naked Streptoneura, *Entoconcha*, *Enteroxenos*, *Pterotrachea*, *Firoloida* also have an operculated shell in the larval stage of development. Among the Euthyneura, on the other hand, only *Actaeon* and *Limacina* among the Opisthobranchs, and *Amphibola* among the Pulmonates, possess an operculum in the adult stage, but the great majority, even of the naked

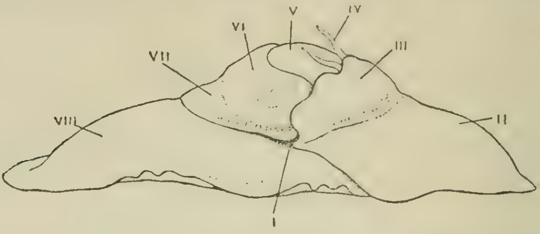


Fig. 47.

Natica josephina, fully expanded; right-side view. I, exhalant orifice; II, propodium; III, part of propodium reflected on the shell; IV, tentacles; V, shell; VI, posterior part of foot reflected on the shell; VIII, hind-part of the foot. (After Schiemenz.)

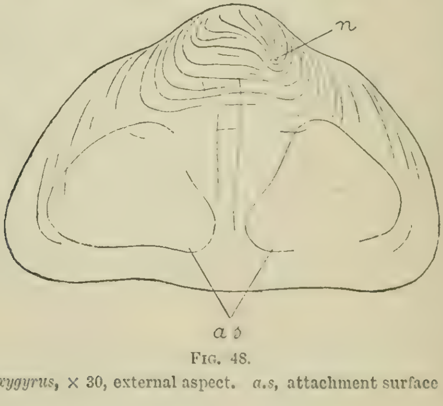


Fig. 48.

Operculum of *Oxygyrus*, × 30, external aspect. *a.s*, attachment surface; *n*, nucleus of the opercular spire.

forms such as the Nudibranchs, the Cymbuliidae, and *Pleurobranchus*, are provided with an operculated shell during their development, the only exceptions being some highly specialised forms, *e.g.* the Pulmonates (excepting the Auriculidae, Siphonariidae, and Oncidiidae, which have an operculum during development), *Runcina*, *Cenia*, and of the "Pteropods," the Cavoliniidae and Gymnosomata.

An operculum may be present or absent in the adults of the same genus, as may be seen in *Stomatella*, *Vermetus*, *Voluta*, *Mitra*, *Pleurotoma*, and *Conus*. It may be absent in certain individuals of the same species as in *Volutharpa ampullacea*, or it may be normally caducous in aged individuals as in *Limacina antarctica* and *L. helicina*. The composition of the operculum varies very much in the different groups of Gastropoda. It is commonly horny, or it may consist of a horny plate covered by a thin calcareous layer, as in *Liotia* among the Delphinulidae and *Cistula* among the Cyclostomatidae; or, finally, it may be completely calcified, as in the Turbinidae, Phasianellidae, Neritidae, etc. Its conformation is originally spiral, and in this case the spire is always inverse to that of the shell, even in the Atlantidae (Fig. 48), except in certain cases of hyperstrophy described below. It may, however, be concentric, imbricated, or scaly (Strombidae, Fig. 75, *op*), and it may be furnished with lateral apophyses as in *Neritina*, *Rissoina*, and *Stira*. Some non-operculate testaceous Gastropods, as, for instance, many stylommatophorous Pulmonates and some species of Planorbis, secrete glutinous or calcareous epiphragm which closes the mouth of the shell during hibernation or aestivation. In *Hipponyx* the foot secretes a calcareous plate by means of which the animal fixes itself to the substratum.

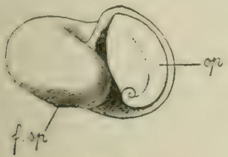


FIG. 49.

Limacina antarctica, young specimen with the operculum *in situ*. *f.sp*, false spire; *op*, operculum.

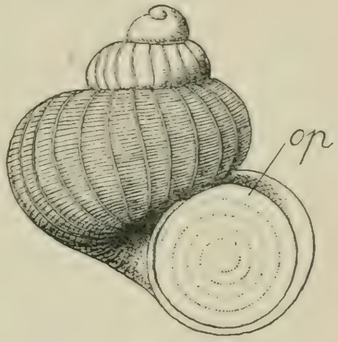


FIG. 50.

Cyclostrema decussatum. Shell and operculum (*op*).

2. *Visceral Sac, Mantle, and Shell.*—The mantle normally covers the whole of the visceral sac and projects all round it, leaving only the head and foot projecting on the ventral side. On the anterior or on the lateral aspect, or exceptionally on the posterior aspect, as

in the Cavoliniidae and Cymbuliidae, there is a space left between the mantle and the body, constituting the *pallial cavity*. This pallial cavity has a situation opposite to that which it occupies in other Molluscs (Fig. 22), due to the torsion which the Gastropod body undergoes towards the end of its development.

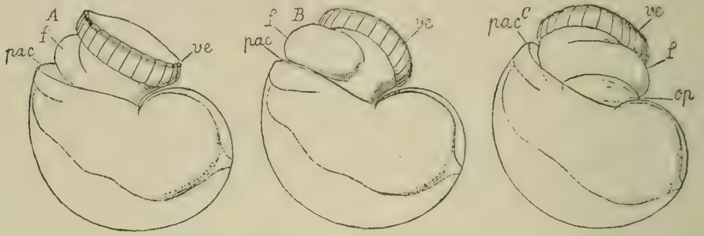


Fig. 51.

Three larvae (veligers) of *Trochus*, during the process of torsion, viewed from the right side of the shell. *A*, nearly symmetrical larva; *B*, a stage 1½ hour later than *A*; *C*, a stage 3½ hours later than *B*. *f*, foot; *op*, operculum; *pa.c*, pallial cavity; *ve*, velum. (After Robert.)

The process by which this torsion is brought about may be referred, on ultimate analysis, to a morphological phenomenon common to the Cephalopods (Fig. 119, D), Scaphopods (Fig. 119, B), and Lamellibranchs (Fig. 119, C), as well as to the Gastropods. This phenomenon is the ventral flexure which takes place in an antero-posterior sagittal plane, about a transverse axis situated at right angles to the main antero-posterior axis of the animal, and results in the approximation of the two ends of the digestive canal. As a consequence of this flexure, the visceral mass and shell, which were originally saucer-shaped, become thimble-shaped, or are produced into a more or less pointed cone, and during the flexure there is a simultaneous coiling of the visceral sac and the shell covering it in a dorsal or anterior direction, so that an exogastric coil is produced.

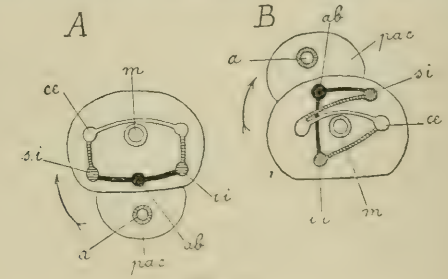


Fig. 52.

Diagram of the torsion of the visceral commissure in the Streptoneura seen from the buccal side. *A*, before the torsion, whose direction is indicated by the arrow; *B*, after the torsion. *a*, anus; *ab*, abdominal ganglion; *ce*, cerebral ganglion; *i.i*, infra-intestinal ganglion; *m*, mouth; *pa.c*, pallial cavity; *s.i*, supra-intestinal ganglion.

as may be seen in the Patellidae, Fissurellidae, and Trochidae (Fig. 51, A). This disposition of the shell is the same as that which obtains in other Molluscs with coiled shells (Nautilidae, Fig. 270), but without lateral torsion. But in Gastropods, during the completion of the metamorphosis, there is a lateral torsion subsequent to the primitive ventral flexure, as a result of which the originally dorsal or exogastric shell becomes ventral or endogastric (Fig. 51, C). This lateral torsion is causally connected with the growth of the ventral creeping surface, which primitively was very short, but eventually increases in length, and in so doing tends again to remove the pallial opening, and with it the anal and renal orifices and the respiratory organs, away from the head. The approximation of these organs to the head is therefore necessarily effected by a lateral torsion in a plane perpendicular to the primitive ventral flexure; that is to say, about a dorso-ventral axis situated in the same median sagittal plane as the antero-posterior axis. It is this second lateral torsion, then, involving all the organs contained in the shell—the cephalo-pedal mass being supposed to be fixed or *vice versa*—which brings the pallial aperture and the anus from a posterior to an anterior position (Fig. 53).

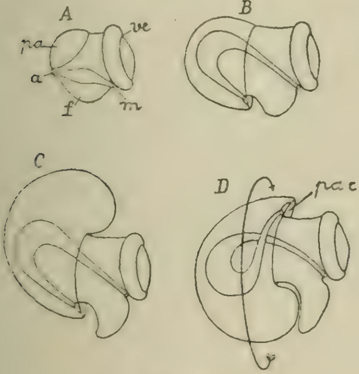


FIG. 53.

Four stages of the development of a Gastropod, showing the process of the body-torsion. *A*, embryo without flexure; *B*, embryo with ventral flexure of the intestine; *C*, embryo with ventral flexure and an exogastric shell; *D*, embryo with lateral torsion and an endogastric shell (the arrows indicate the direction of the torsion). *a*, anus; *f*, foot; *m*, mouth; *pa*, mantle; *pa.c*, pallial cavity; *ve*, velum. (After Robert.)

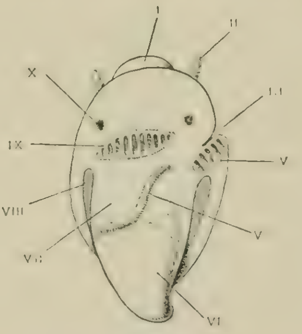


FIG. 54.

Scissurella lytteltonensis, out of its shell, dorsal aspect. I, snout; II, right tentacle; III, pallial slit; IV, right gill; V, rectum; VI, gonad; VII, left kidney; VIII, left half of the columellar muscle; IX, left gill; X, left eye.

During this lateral torsion the following changes are necessarily produced in the original organisation of Gastropods:—(1) The anus being carried forward along one side of the animal, the organs situated on either side of this orifice change their relative positions; those which were morphologically on the right become topographically on the left side, and *vice versa*. (2) The visceral commissure, while maintaining its position in respect to the digestive canal, becomes twisted (Fig. 52) in such a manner that its right moiety with its ganglion passes over to the dorsal side of oesophagus (Fig. 57), and is therefore called *supra-intestinal*, while the left moiety passes under the oesophagus towards the right side, which explains the name infra-intestinal given to this portion of the commissure and the nerve-centre borne on it. (3) The original symmetry of the organisation disappears. The anus does not remain in the centre of the pallial cavity, but is displaced towards the right side. The organs situated on the topographically right—but morphologically and originally left—side atrophy (*Pleurotomaria*, *Scissurella*, etc.), and eventually disappear. An essential feature of the asymmetry of Gastropods is the atrophy or disappearance of the topographically right (morphologically left) half of the circumanal complex, involving the ctenidium, auricle, osphradium, hypobranchial gland, and kidney. In forms with *situs inversus*, or, as they are generally called, sinistral forms, the phenomenon is reversed: the organs of the left side are preserved, those of the right side atrophy or disappear. In dextral Gastropods the only structure found on the topographically right side of the rectum is the genital orifice. But this is not an original organ. It is wanting in forms which, like *Pleurotomaria*, *Haliotis*, etc., have preserved the maximum of symmetry. Moreover, in the most primitive stage of organisation, the gonads opened into the kidneys. As soon as the asymmetry makes its appearance, even while there are yet two kidneys, the genital products are conducted only into the right kidney (Patellidae, Trochidae, Fig. 55, Fissurellidae). Consequently the right kidney cannot disappear altogether, but persists in part as the gonaduct. The latter structure, therefore, is the remains of the topographically right kidney, a view which

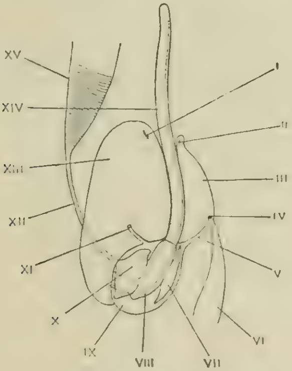


FIG. 55.

Trochus cinerarius, heart and kidneys, dorsal aspect (somewhat schematic). I, left renal pore; II, right renal pore; III, right kidney; IV, papilla with the common opening of the pericardium and of the gonad into the right kidney; V, right renopericardial duct; VI, anterior part of the gonad; VII, right auricle; VIII, ventricle; IX, pericardium; X, left auricle; XI, left reno-pericardial orifice; XII, branchial efferent vessel; XIII, left kidney; XIV, rectum; XV, gill.

has been confirmed by the study of the embryology of *Paludina*. (4) The coil of the visceral sac and shell becomes endogastric. Originally these structures were coiled dorsally or, in other words, were exogastric (Fig. 53, C), but as a result of a rotation through an angle of 180°, the coil necessarily becomes ventral or endogastric (Fig. 53, D). Most usually, however, the coils of the visceral sac and shell do not remain in the same plane, but the summit of the spire gradually comes to project on the side which was originally left, but which at the end of development is finally and topographically right (Fig. 44). Thus a spiral coil is formed which has the advantage of giving a more compact form to the shell and its contents, and of diminishing its diameter. In those forms in which the torsion and asymmetry is dextral, the coil of the spire is conformable since it also is dextral; that is to say, it follows the direction of the hands of a watch if the shell is viewed from the summit of the spire (Figs. 47 and 132, etc.). Nevertheless, the coil of the shell is by no means the cause of the torsion; both are foreshadowed in the segmentation of the ovum, in which there is a complete reversal of the direction of the cleavage planes in sinistral as compared with dextral Gastropods. The apparent direction of the coil, however, may be changed by a process of hyperstrophy (see below, p. 82), and finally the coil of the visceral mass and spire may disappear in the adult, leaving the internal torsion and asymmetry unaltered, but producing a secondary external symmetry, as in the Patellidae (Fig. 56), Fissurellidae, etc. (5) By detorsion, or movement in a contrary direction, the anus and circumanal complex (with the exception of the male or hermaphrodite genital aperture) may be carried back to a posterior posi-

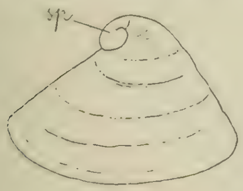


FIG. 56.

Shell of a very young *Patella vulgata*, viewed from the right side, × 25. *sp*, apical spire.

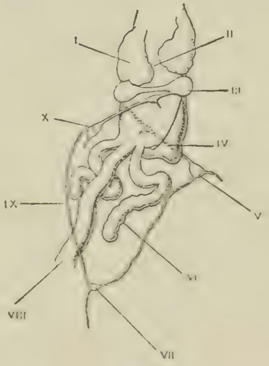


FIG. 57.

Nervous system of *Actaeon tornatilis, in situ*, dorsal aspect. I, buccal gland; II, buccal mass; III, cerebral ganglion; IV, infra-intestinal part of the visceral commissure, with a small pallial ganglion; V, infra-intestinal ganglion; VI, right salivary gland; VII, abdominal ganglion and genital nerve; VIII, oesophagus; IX, supra-intestinal part of the visceral commissure; X, supra-intestinal ganglion.

tion. This tendency to detorsion may be observed in exceptional cases among the Streptoneura (*Pterotrachea*, Fig. 143), but it is specially characteristic of the whole group of the Euthyneura, leading to the untwisting of the visceral commissure, which, in this group, is obviously twisted only in *Actaeon* (Fig. 57). When detorsion is carried to its extreme limit as in *Pterotrachea*, it is accompanied by a reduction or disappearance of the mantle and visceral sac and opisthobranchialism. In the least specialised Opisthobranchs and Pulmonates the detorison is not complete, and the pallial aperture is carried only to the right side (Figs. 148, 67); but in the most specialised forms the anus and the pallial cavity (if the latter is retained) are moved back to the posterior extremity of the body, as in *Philine* (Fig. 58), *Aplysia* (Fig. 154), Doridomorpha (Fig. 79), and many other Nudibranchs, such as *Janus*, *Alderia*, *Limapontia*, and *Cenia*; and among Pulmonates in *Testacella*, *Vaginula* (Fig. 179), and *Oncidium* (Fig. 59). In this manner a secondary external symmetry is re-established. The detorsion of the organism is complete in the Tectibranch Cavoliniidae ("straight Thecosomatous Pteropods"), in which one may recognise a torsion of 180° in a direction opposite and equal to that of the original torsion, the result of which is that the genital duct is twisted round the alimentary canal and the pallial cavity is shifted to the ventral surface (Fig. 60). It should

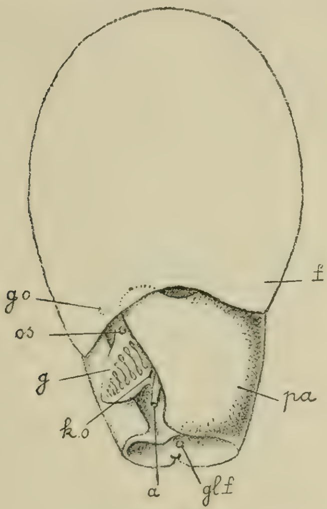


FIG. 58.

Philine aperta, ventral aspect. *a*, anus; *f*, foot; *g*, gill; *gl.f*, glandular fossa; *g.o*, genital orifice (seen through the foot); *k.o*, renal pore; *os*, osphradium; *pa*, inferior pallial lobe. (After Guiart.)

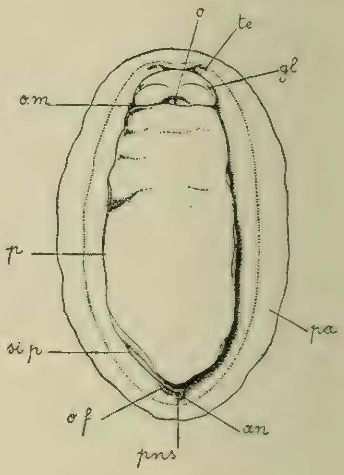


FIG. 59.

Oncidiella patelloides, ventral aspect. *an*, anus; *gl*, tentacular gland; *o*, mouth; *o.f*, female orifice; *o.m*, male orifice; *p*, foot; *pa*, mantle; *pns*, pulmonary orifice; *si.p*, lateral groove; *te*, tentacle.

be noted that in those Euthyneura which are detorted in the adult condition, the primitive torsion is manifest in the course of development, and in the larvae the pallial cavity is anterior and dorsal, the anus anterior, just as is the case in an adult Streptoneura (Fig. 61).

The pallial cavity normally contains the apertures of the anus and the renal ducts; and, as it also contains the ctenidial branchiae, together with their sensory organ, the osphradium, it constitutes the respiratory cavity. There is, in addition, between each branchia and the rectum a more or less differentiated glandular region known as the *hypobranchial gland* or pallial mucous gland (Figs. 75 and 85), which is characteristic of aquatic species. Two such glands are found, one on either side of the rectum, in various Rhipidoglossa, such as *Pleurotomaria* (Fig. 127), *Haliotis*, *Turbo*, etc., but only one, namely, that of the left side, in the majority of aquatic Gastropods with a well-developed mantle. This glandular organ becomes median and nearly symmetrical in the Cavoliniidae (Fig. 60) and the Cymbuliidae.

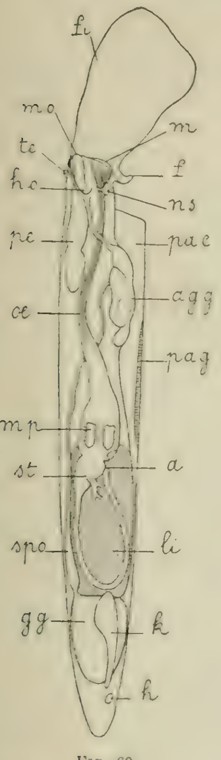


FIG. 60.

Clio striata, removed from its shell, with the head above, right-side view. *a*, anus; *a.g.g*, accessory genital glands; *f*, foot (posterior lobe); *fi*, left fin (the right one is cut away); *gg*, gonad; *h*, heart; *h.o*, hermaphrodite orifice; *k*, kidney; *li*, liver; *m*, mouth; *m.o*, male orifice; *m.p*, masticatory stomachal plate; *n.s*, central nervous system; *oe*, oesophagus; *pa.c*, pallial cavity; *pa.g*, pallial gland; *pe*, penis; *spo*, spermoviduct; *st*, stomach and bile-duct; *t*, right tentacle.

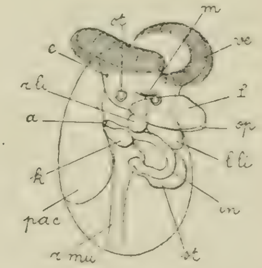


FIG. 61.

Veliger of *Eolis* (*Galvina*) *picta*, ventral view. *a*, anus; *e*, right eye; *f*, foot; *in*, intestine; *k*, kidney; *l.li*, left liver lobe; *m*, mouth; *op*, operculum; *ot*, right otocyst; *pa.c*, pallial cavity; *r.li*, right liver lobe; *r.mu*, retractor muscle; *st*, stomach; *ve*, velum.

The pallial cavity is largely open in the Streptoneura; its orifice is narrower in the Tectibranchs (Fig. 148, IV), and is much reduced in the Pulmonates (Figs. 67 and 177), as the result of the almost complete fusion of the mantle border with the neck.

The mantle border projects somewhat beyond the shell that covers it, and may be furnished with little tentacles, with glands and pigment spots. The border is not continuous in the most archaic forms, but presents in the median line, or at a neighbouring point morphologically equivalent to the median line, a more or less deep longitudinal slit, as may be seen in the Pleurotomariidae (Figs. 54, 127, and 128), in *Emarginula*, and *Scutum*. This slit corresponds in position with the extremity of the rectum, and admits of a more rapid expulsion of the excrements and the respiratory fluid. The edges of the slit may fuse together at one or more points, leaving one or more orifices in the mantle and in the shell on the dorsal side of the pallial cavity (Fig. 62), as in *Fissurella*, *Puncturella*, and *Haliotis*. An analogous slit is also present in *Siliquaria* and *Pleurotoma*. In the female *Vermetus* there is a median slit in the border of the mantle (Fig. 45), but no corresponding fissure in the shell; in this case the mantle slit admits of the fixation of the eggs to the internal wall of the shell, to which they remain attached up to the time of hatching.

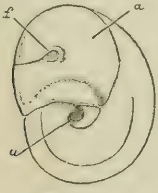


FIG. 62.

Schismope lacuniformis, seen from the umbilicus. *a*, aperture of the shell; *f*, foramen; *u*, umbilicus. (After Watson.)

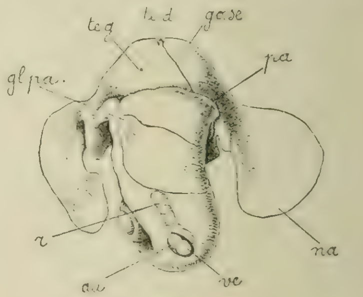


FIG. 63.

Limacina antarctica, removed from its shell, dorsal aspect. *au*, auricle; *gl.pa*, pallial gland; *go.se*, seminal groove; *na*, right fin; *pa*, mantle; *r*, kidney; *te.d*, right tentacle; *te.g*, left tentacle; *ve*, ventricle of heart.

At the left or anterior corner of the pallial aperture the mantle edge is often produced into a tube with a ventral slit (Fig. 99, XV); this tube or siphon serves to admit water into the pallial cavity. A siphon exists only in specialised Streptoneura: it is but slightly developed in the Cerithiidae, is rather larger in the Strombidae (Fig. 75, *si*), and attains its greatest dimensions in the Cassididae and Doliidae and in all the Rachiglossa and Toxiglossa. In the Volutidae the siphon is furnished with an internal appendage. *Ampullaria* also possesses a long siphon, which may serve either for pulmonary or for branchial respiration. On the right side of the pallial opening the mantle border sometimes bears a tentacle, as in *Valvata* (Fig. 132), *Oliva*, *Strombus*, *Acera*, and *Gastropteron*. In *Adeorbis* there are two such tentacles (Fig. 133). In many Tectibranchs the mantle edge at the right side of the pallial opening bears a large *inferior pallial lobe* (Fig. 148, I), which forms the "balancer" in the Thecosomata. This lobe is also found in the basommatophorous or aquatic Pulmonates, and in some species of this group it is converted into a pallial branchia (Figs. 89 and 175).

The dorsal surface of the mantle secretes a shell, formed of a single piece, which necessarily reproduces the form of the mantle, or rather of the visceral sac contained in the mantle. As the visceral sac is always coiled (even in forms with conical shells like the Patellidae and Fissurellidae and in the various Gastropods which are naked when adult the visceral sac is coiled during development), it follows that the shell is also coiled. The curvature of the coil, or conchospiral, is, generally speaking, a logarithmic spiral. The spire, that is to say, the totality of the whorls, with the exception of the last formed, may be excessively prominent, as, for example, *Terebra*, *Turritella*, *Turbonilla*, certain Cerithiidae, etc., or may exhibit every possible disposition, until the prominence disappears and the shell becomes discoidal as in *Planorbis*, *Atlanta* (Fig. 141), etc.

The various whorls of the spire are normally contiguous, but it occasionally happens that, after a certain number of turns, the visceral mass and the shell appear to unroll more or less completely, and to continue their course either in a much looser spiral or in a slightly curved line, or even in a nearly straight line (*Vermetus*, Fig. 45, *Magilus*, *Cyclosurus*, *Caecum*, Fig. 68). The extremity of the last whorl may also form a certain angle with the direction of the preceding whorls, as, for example, in certain helicomorphous Pulmonates (*Anostoma*).

The coil, commencing from the initial point of formation or summit, is dextral when the shell, held with the summit towards the observer, has the mouth or aperture below and to the right. It is sinistral when, under the same conditions, the aperture is to the left. Dextral shells are much more common than sinistral.

This direction of the coil, when it is not obscured by "hyperstrophy," is conformable with that of the asymmetry of the organisation: that is to say, a sinistral coil corresponds completely to the *situs inversus viscerum* of a dextral Gastropod. This *situs inversus* may be seen in the genera *Triforis*, *Laeocochlis*, *Actaeonia*, *Blauneria*, *Clausilia*, *Physa*; in certain species of the genera *Fulgur*, *Neptunea*, *Bulimulus*, *Helicter*, *Vertigo*, *Ariophanta* (*Nanina*), *Ancylus*, *Diplommatina*; and in some teratological individuals of *Buccinum undatum*, *Littorina littorea*, *Neptunea antiqua*, *Limnaea stagnalis* (in which the monstrosity has been sometimes fixed by heredity), *Helix*, *Arion*, and various other Pulmonates. There are, however, forms in which the coil is hyperstrophic: in this case the whorls which form the spire are very slightly prominent; the spire becomes flatter and flatter, and finally becomes concave and is transformed into a false umbilicus. At the same time the part corresponding to the umbilicus (the cavity opposite to the spire) of normally coiled forms becomes prominent and constitutes a false spire. The coil then appears to be sinistral, although the asymmetry of the organisation remains dextral, as, for example, in *Lanistes* and the coiled thecosomatous Pteropods, in which the opercular spiral follows the same direction as the apparent spire of the shell (Fig. 49); or reciprocally in *Planorbis*, especially in individuals which are scalariform or teratologically unrolled, such as *Choanomphalus* and *Pompholyx* (Fig. 64). Finally, it may sometimes be observed that the spiral in which the coil is formed insensibly changes its nature or its apparent direction after the first larval whorls are completed. This is the phenomenon of heterostrophy, in which the spiral from being negative eventually becomes positive; that is to say, the coil that was at first hyperstrophic becomes finally orthostrophic. Examples of this phenomenon are *Solarium* (the larval shell of which has been called *Agadina*), *Mathilda*, the Pyramidellidae (Fig. 65), *Melampus*, and various Bullidae.

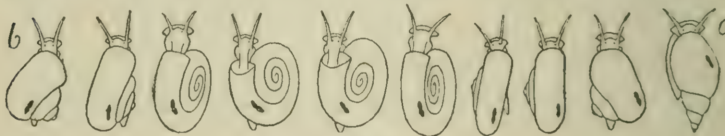


Fig. 64.

Passage from a sinistral orthostrophic form (*a*) to a pseudo-dextral hyperstrophic one (*b*); the heart is indicated in black, in order to show the constancy of the sinistral organisation. (After J. W. Taylor.)

The line along which two successive whorls of the shells cease to be in contact with one another is the "suture." The portion of the shell separating the successive whorls of the visceral spire may be resorbed in certain cases (many Auriculidae, some Neritidae, *Cypraea*, *Olivella*, etc.), resulting in the concrescence of the whorls of the visceral sac, or even in the suppression of its coils, as may be seen in several species of the genus *Auricula* (Fig. 67). On the other hand, the animal may desert the first whorls of the coiled shell, and cut itself from them by the formation of a transverse partition or septum: this operation may, in certain cases, be repeated several times, *e.g.* *Vermetus*, *Turritella*, *Caecum* (Fig. 68), *Truncatella*, *Triton* (Fig. 66), *Cuvierina*, etc. In the families Cylindrellidae, Stenogyridae (*Rumina decollata*), and Pupidae, and in the genera *Truncatella*, *Cerithidea*, *Caecum*, and *Cuvierina*, the portion of the shell beyond the septum may be truncated and lost, or the first whorls may be filled up by a calcareous deposit as in *Magilus*. In the conical shell of various Capulidae (Taenioglossa), *Zeidora*, and *Septaria* (Rhipidoglossa) and *Latia* (Basommatophora) there is an incomplete internal septum, corresponding to the interior margin of the aperture, which has become prominent. In certain genera this septum is folded into the shape of a trumpet, the cavity of which affords a lodgment for a projection of the posterior part of the foot (*Crucibulum*, Fig. 69). In the last whorl of the shell of *Clausilia* there is an accessory piece, the clausilium, attached to the columellar axis by an elastic support: this piece closes the mouth of the shell when the animal

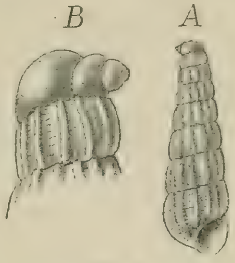


Fig. 65.

Odostomia dipsycha. *A*, the entire shell, seen from the aperture side; *B*, the heterostrophic apex, more magnified. (After Watson.)

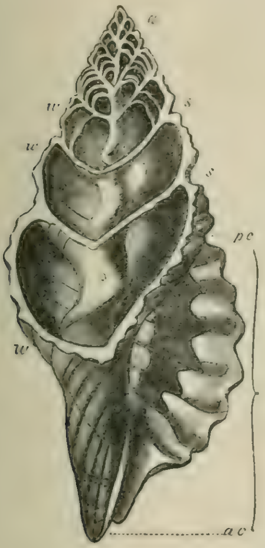


Fig. 66.

Section of the shell of *Triton*. *a*, *apex*; *a.c*, anterior canal (or siphon) of the aperture of the shell (*a.c* to *p.c*, aperture of the shell); *p.c*, posterior canal of the aperture; *s*, sutures of the whorls; *w*, whorls of the shell; occupying the axis, and exposed by the section, is seen the "columella" or spiral pillar. The upper whorls of the shells are seen to be divided into separate chambers by the formation of successively formed "septa." (From Lankester, after Owen.)

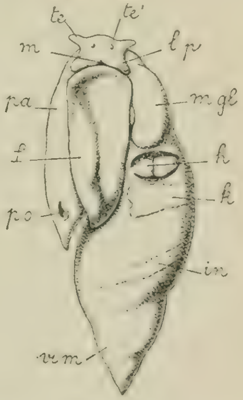


Fig. 67.

Auricula (*Alexia*) *bidentata*, removed from its shell, ventral aspect. *f*, foot; *in*, intestine; *k*, kidney; *l.p*, labial palp; *m*, mouth; *m.gl*, pallial gland opening into the pallial cavity; *pa*, mantle; *p.o*, pneumostome or pulmonary orifice; *te*, posterior tentacle; *te'*, rudimentary anterior tentacle; *vi.m*, visceral mass, whose different whorls are fused together.

is retracted, but is pushed back against the axis when the animal is extended.

The Gastropods are attached to their shells by the columellar muscle (Fig. 45, *co*), and withdraw themselves into their shells by its contraction. This muscle is symmetrical and horseshoe-shaped in species with conical shells (*Patella*, *Septaria*, *Capulus*, etc.), but in other species it is asymmetrical. It is oval in *Haliotis*, and its insertion on the columella is nearly linear in coiled forms. The power of this muscle is often considerable: in *Patella vulgata* it can resist a traction of fifteen kilograms. The columellar muscle is naturally absent in forms without shells (Nudibranchs, *Oncidium*, *Vaginula*), but is present in *Testacella*.

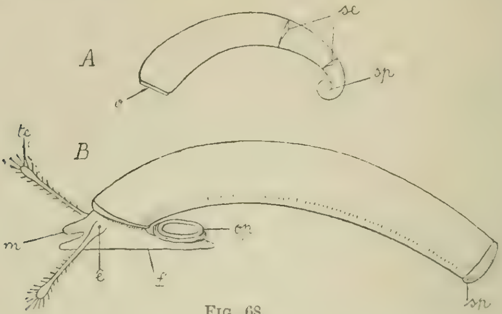


FIG. 68.

Caecum. *A*, entire shell, left-side view. *o*, aperture; *sc*, septa; *sp*, spire. (After de Folin.) *B*, animal with truncated shell. *e*, eye; *f*, foot; *m*, mouth; *op*, operculum; *sp*, septum; *tc*, tentacle. (After Plate.)

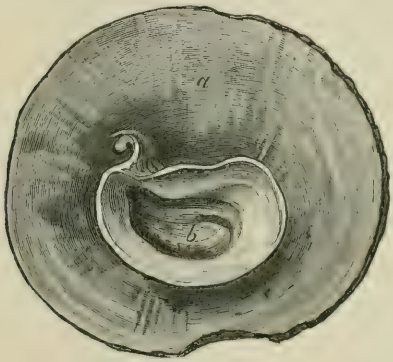


FIG. 69.

Shell of *Crucibulum*, seen from below, showing the inner whorl *b*, concealed by the cap-like outer whorl, *a*. (From Lankester.)

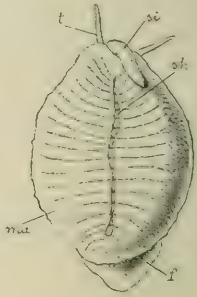


FIG. 70.

Cypraea europaea, dorsal view, × 3. *f*, foot; *ma*, mantle; *sh*, shell; *si*, pallial siphon; *t*, tentacle.

3. *Origin of Naked Forms.*—In many cases the borders of the

mantle are reflected over the shell and cover a greater or less part of its external surface. This condition is found in various Fissurellidae (*Fissurellidea*), in *Marsenina*, in many Cypraeidae (Fig. 70) and Marginellidae, in *Pyrula* (Fig. 71), *Aplysia* (Fig. 154), many Bullidae, and various Pulmonates, such as *Vitrina*, *Parmarion*, *Hemphillia*, *Homalonyx*, *Amphipeplea*, etc. The portion of the internal surface of the mantle that has thus become external may bear more or less well-developed and ramified appendages (*Cypraea*), and the other surface of the reflected mantle may sometimes secrete an external coating of enamel over the portion of the shell to which it is applied. The borders of the mantle, extending more and more over the shell, may finally meet, unite, and thus form a closed sac containing the shell, which, together with the visceral sac contained in it, suffers a diminution, or even an almost complete disappearance, of its spiral form, so that the animal appears to be quite naked. This condition may be seen in *Pupilia* among the Fissurellidae, in the majority of the Lamellariidae, in *Pustularia* among the Cypraeidae, in many Tectibranchs, such as *Notarchus*, *Doridium*, *Gastropteron*, *Philine*, *Pleurobranchus*, and in sundry limaciform Pulmonates. In some cases the shell-sac remains in communication with the exterior by means of a fine ciliated canal, situated at the posterior end of the body (*Philine*, *Doridium*). In the Tectibranchs the internal shell is often very slightly calcified, and at the same time the pallial cavity becomes more and more reduced. Finally, the shell and the shell-cavity disappear, leaving the mantle absolutely naked

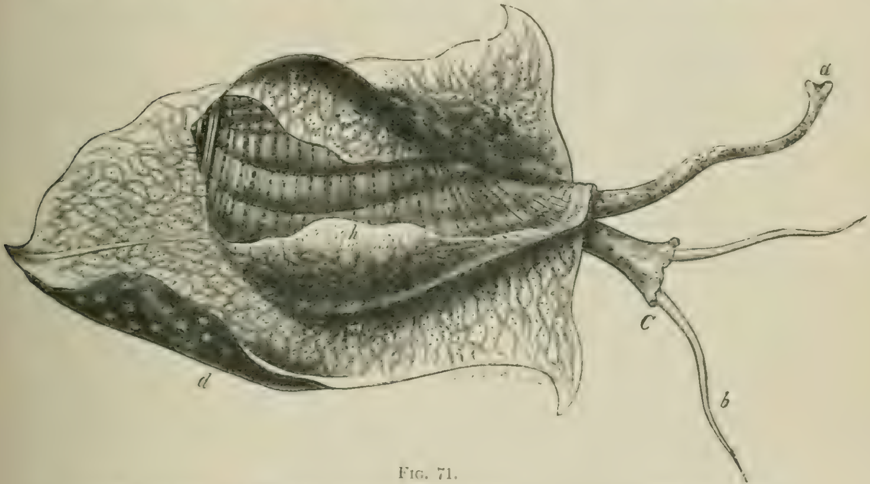


Fig. 71.

Animal and shell of *Pyrula laevigata*, seen from above. *a*, siphon; *b*, head-tentacles; *C*, head; *d*, foot, expanded as in crawling; *h*, the mantle-skirt reflected over the sides of the shell. (From Lankester, after Owen.)

and without a spiral coil. At the same time there is a return to a secondary external symmetry. This phenomenon may be seen in the Titiscaniidae, *Pterotrachea* (Fig. 143), *Runcina*, *Phyllaplysia*, the gymnosomatous "Pteropods" (Fig. 84), the Cymbuliidae (Fig. 151), *Pleurobranchaea* (Fig. 157), the Nudibranchs (Figs. 160, 161, etc.), the Philomycidae, the Oncidiidae (Fig. 59), and the Vaginulidae (Fig. 179). In these cases, excepting *Cenia* and *Runcina*, the shell exists only during development, and falls off at the close of larval life. As a rule, the pallial cavity is reduced at the same time (*Pterotrachea*, *Pleurobranchaea*, *Gastropteron*), or it may disappear together with the ctenidium, and the external surface of the dorsal visceral envelope may give rise to various appendages such as the cerata or dorsal "branchial" papillae of Nudibranchs (Fig. 160, A, *c*) and the terminal branchia of the Gymnosomata (Fig. 84, VII). In one instance in which the larval shell is caducous a second persistent shell is formed, covered by the mantle: such is the case in *Lamellaria*, whose primary shell is covered with spines, and was formerly believed to belong to another animal to which the name of *Echinospira* was given.

In parasitic Gastropods the naked condition of the adult is the result of an essentially similar process, but the shell is covered over by a cephalic expansion known as the "pseudopallium" (Fig. 20, *ps*). Finally, the nudity of certain "Heteropods" (Pterotracheidae) is due to the progressive reduction of the visceral sac and the disappearance of the mantle. In many Gastropods that are naked in the adult condition calcareous spicules of some size are developed in the sub-epithelial conjunctive tissue of the mantle, *e.g.* in the Pleurobranchidae and in Doridomorpha, the Hedylidae among the Nudibranchs. In the Cymbuliidae (Fig. 151, II) the sub-epithelial connective tissue gives rise to a pseudo-conch.

II. Anatomy.

1. *The Alimentary Canal.*—This comprises, in the various forms of Gastropods, a buccal cavity connected by the oesophagus with a stomachal cavity, and an intestine properly so-called, the last-named being tolerably long and coiled. The buccal cavity and the oesophagus are of ectodermic origin, and taken together form the fore gut. The buccal cavity normally opens at the extremity of the head, which generally has the form of a cylindrical snout slightly inflected towards the ventral surface (Fig. 130, VI). In many cases, however, the opening of the buccal cavity is carried backward by the development of an invagination of the pre-oral integuments, and thus an apparent mouth is formed which is not morphologically equivalent to the true mouth, the latter being carried to the anterior extremity only by an evagination of the

tegumentary ingrowth, which in this manner gives rise to a proboscis. When this extensible proboscis is evaginated the oesophagus forms its interior lining; when it is invaginated the oesophagus forms its posterior continuation. Such is the pleurecbolic proboscis of Ray Lankester (Fig. 72) found in the Cypraeidae, Naticidae, Lamellariidae, Scalariidae, *Vermetus*, the Capulidae, Calyptraeidae, Strombidae, and Chenopodidae among the Streptoneura, and in some Opisthobranchs, viz. *Doridium*, the Pleurobranchidae, *Aplysia*, the Gymnosomata, and the Doridopsidae. In other cases the proboscis cannot be wholly retracted, and then the

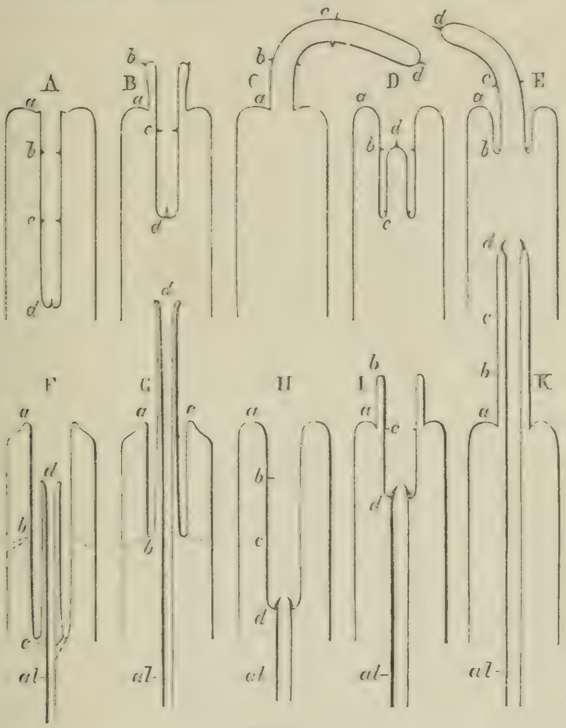


FIG. 72.

Diagrams explanatory of the nature of so-called proboscides or "introverts." *A*, simple introvert completely introverted. *B*, the same, partially everted by eversion of the sides, as in the Nemertine proboscis and Gastropod eye-tentacle = pleurecbolic. *C*, the same, fully everted. *D*, *E*, a similar simple introvert in course of eversion by the forward movement, not of its sides, but of its apex, as in the proboscidean Rhabdocoels = acrecbolic. *F*, acrecbolic (= pleurembolic) introvert, formed by the snout of the proboscidiferous Gastropod. *al*, alimentary canal; *d*, the true mouth. The introvert is not a simple one with complete range both in eversion and introversion, but is arrested in introversion by the fibrous bands at *c*, and similarly in eversion by the fibrous bands at *b*. *G*, the acrecbolic snout of a proboscidiferous Gastropod, arrested short of complete eversion by the fibrous band *b*. *H*, the acrembolic (= pleurecbolic) pharynx of a Chaetopod fully introverted. *al*, alimentary canal; at *d*, the jaws; at *a*, the mouth; therefore *a* to *d* is stomodaeum, whereas in the Gastropod (*F*) *a* to *d* is inverted body surface. *I*, partial eversion of *H*. *K*, complete eversion of *H*. (After Lankester.)

wall of the digestive tube is folded twice on itself during invagination. This is the pleurembolic proboscis of Ray Lankester (Fig. 72) found in the Rachiglossa (Fig. 99, XIII), in certain Toxiglossa, and in the Doliidae, Cassididae, and Tritonidae among the proboscidiferous Taenioglossa. In the Naticidae there is a glandular disc on the ventral face of the proboscis which serves to perforate the shells of the Lamellibranchs on which they feed, and in the Pneumodermatidae there are suckers in the same position situated on two retractile lobes and either isolated or united to one another.

The mouth leads into the buccal or pharyngeal cavity, which is the first of the principal dilatations of the digestive tract. The salivary glands open into it, and the chitinous masticatory sclerites are attached to its walls. The whole, together with the muscular masses which actuate the masticatory apparatus, forms the buccal bulb or pharynx (Fig. 74, A), situated behind the oesophageal nerve-collar in the more archaic species, but in front of it in the more specialised Gastropoda (Fig. 146). In some carnivorous forms, such as *Glandina* and *Testacella*, the pharynx may be more or less completely evaginated, forming a false pleurecbolic proboscis. The chitinous buccal sclerites are of two kinds, mandibular and radular.

(1) *The mandibles* are solid cuticular thickenings situated at the anterior end of the buccal cavity. In the majority of Streptoneura and Opisthobranchs they are paired, the members of the pair being lateral and symmetrical (Fig. 73, A); they are smooth or scaly, generally with trenchant, but sometimes with denticulated margins. These paired mandibles are usually quite separate from one another, but in the Naticidae they are in contact dorsally, and in *Lamellaria* they are clearly fused together on the dorsal side to form a single piece. Similarly there is only a single median mandible formed by the fusion of two symmetrical pieces in the Patellidae, in *Aegirus* (Doridomorpha, Fig. 73, B), and in all the Pulmonates. This median mandible is dorsal, its lower or free border is trenchant, nearly horizontal, and frequently provided with a median projection. Two lateral and symmetrical accessory cuticular thickenings are found in the majority of the basommatophorous Pulmonates (*Limnaea*, *Planorbis*, etc.). In certain Aplysiomorpha in which the mandibles are ventral there is a patch of horny spines on the roof of the buccal cavity (*Notarchus*), and in certain cases these are divided into two symmetrical groups enclosed in diverticula, which have the form of evaginable sacs (Gymnosomata). In the Rachiglossa the mandibles are rudimentary, and they are absent in many

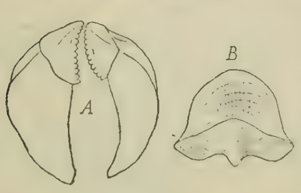


Fig. 73.

Mandibles of Gastropoda. *A*, paired lateral mandibles of *Janus*; *B*, dorsal mandible of *Aegirus*. (After Hancock.)

Trochidae, in *Neritina*, in the Helicinidae, in *Cyclostoma*, in *Thyca*, in the Pyramidellidae, Eulimidae, Entoconchidae, and Coralliophilidae, in all the Toxiglossa, in the Heteropods, in *Actaeon*, *Tornatina*, *Scaphander*, *Doridium*, the Lophocercidae, *Cymbuliopsis*, *Gleba*, *Clione*, *Umbrella*, *Doris*, the porostomatous Doridomorpha, *Tethys*, the Elysiae, *Gadinia*, *Amphibola*, the Testacellidae, etc.

(2) *The radula* is a sort of ribbon of greater or less width, formed of distinct and separate chitinous teeth, borne on a single supporting membrane. It is secreted in a ventral caecum (Fig. 74, A, *n*), in which it is almost wholly contained, but its anterior extremity stretches out on the floor of the buccal cavity, where it forms a median projection (Fig. 74, A, *p*). The radular ribbon is supported by a system of paired cartilaginous pieces furnished with protractor and retractor muscles (Fig. 74, A, *l*, *m*), the action of which causes the radula to move to and fro and work like a rasp on the prey seized by the animal. The teeth are secreted at the bottom of the caecum or sheath of the radula, by a small number of matrix cells; in front of these is a transverse row of cells which secrete the basal membrane. The teeth are disposed in transverse rows, and in each row there is a median tooth called the "central" or rachidian tooth, on either side of which the remaining teeth of the row are symmetrically disposed. In the Euthyneura all the lateral teeth are generally similar to one another (Fig. 145), but in the Streptoneura, when there is more than one tooth on either side, they are divided into two clearly defined groups. The teeth nearest to the central are the "laterals," properly so-called, and differ from the more elongated external teeth, which are known as the "marginals" or uncini (Fig. 2, *m*). The number of teeth in any given transverse row is constant in any given species; it may, however, increase slightly with age, at any rate in various Aplysiidae and in the terrestrial Pulmonates. On the other hand, the number of teeth is variable from group to group, and generally is more considerable in the less specialised than in the more specialised groups. Thus, in the Streptoneura the Rhipidoglossa have numerous lateral teeth on either side of the central; the Taenioglossa have only three lateral teeth on either side, the Rachiglossa only one. Among the Opisthobranchs many teeth are included in each transverse row in *Actaeon* and the Pleurobranchidae, but there are only three in the thecosomatous "Pteropods" and only one in the Elysiae. The number of successive transverse rows also varies from species to species, and consequently the total number of teeth in the radula is very different in different forms. There are sixteen (one tooth in each row) in certain Eolidae and Elysiae; about two hundred and fifty in *Buccinum undatum*; 1920 in *Patella vulgata*; 3500 in *Littorina littorea*; 6000 in *Doris tuberculata*; 8343 in *Limnaea stagnalis*; 15,000 in *Helix aspersa*; 26,800 in *Limax maximus*;

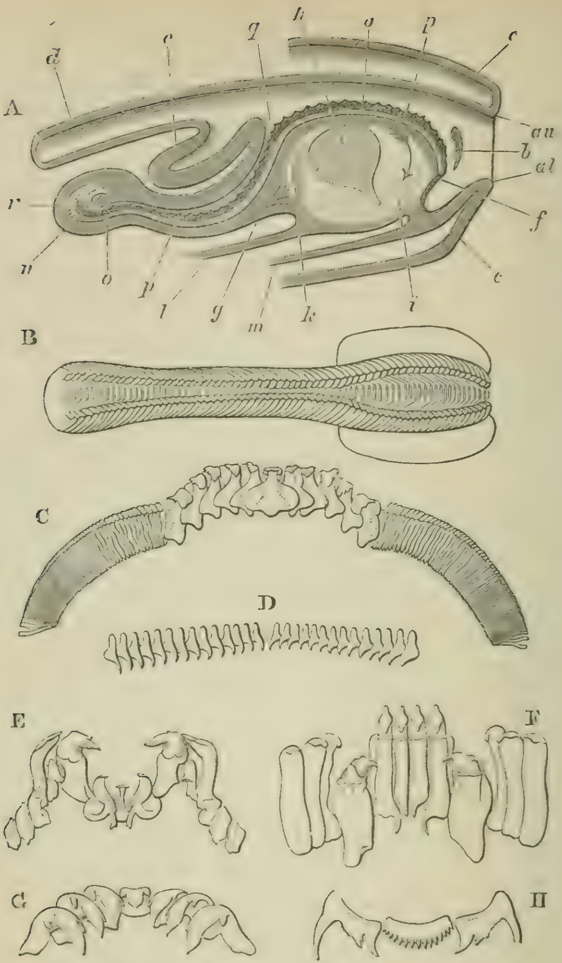


FIG. 74.

Radulae of various glossophorous Mollusca. *A*, diagram showing mouth, oesophagus, and lingual apparatus of a Gastropod in median sagittal section. *a.l*, lower lip ; *a.u*, upper lip ; *b*, jaw of the left side ; *c*, outer surface of the snout ; *d*, oesophagus ; *e*, fold in the wall of the oesophagus behind the radular sac (*n*) ; *f*, anterior termination of the radula and its bed, the point at which it wears away ; *g*, base of the radular sac or recess of the pharynx ; *h*, cartilaginous piece developed in the floor of the pharynx beneath the radula, and serving for the attachment of numerous muscles, and for the support of the radula ; *i*, anterior muscles ; *k*, posterior muscles attached to the cartilage ; *l*, muscle acting as a retractor of the buccal mass ; *m*, muscle attached to the lower lip ; *n*, posterior extremity of the radular sac ; *o*, the bed of the radula or layer of cells by which its lower surface is formed ; *p*, the radula or lingual ribbon ; *q*, opening of the radular sac into the pharynx or buccal cavity ; *r*, cells at the extreme end of the inner surface of the radular sac which produce, as a cuticular secretion, the rows of teeth of the upper surface of the radula.

B, radula or lingual ribbon of *Paludina vivipara*, stripped from its bed.

C, a single row of teeth from the radula of *Trochus cinerarius* (Rhipidoglossate); formula : ∞.5.1.5.∞.

D, a single row of teeth from the radula of *Ianthina fragilis* (Stenoglossate); formula : ∞.0.∞.

E, a single row of teeth from the radula of *Trachydermon cinereum* (Amphineura); formula : 3.1.2.1.1.1.1.1.2.1.3.

F, a single row of teeth from the radula of *Patella vulgata* (Docoglossate); formula : 3.1.2.0.2.1.3.

G, a single row of teeth from the radula of *Cypraea helvola* (Taenioglossate); formula : 2.1.1.1.2.

H, a single row of teeth from the radula of *Nassa annulata* (Rachiglossate); formula : 1.1.1. The common Whelk is similar to this.

36,000 in *Tritonia hombergi*; 40,000 in *Helix ghiesbrechti*; 75,000 in *Susania tuberculata*; and as many as 750,000 in *Umbrella*. It follows that the length of the radular ribbon varies very much; it is considerable in *Cyclostoma* and *Patella* (Fig. 88, *r*), in which it exceeds the length of the body, and in the Littorinidae, in which it is coiled into a spiral so as to occupy less room; in one species, *Tectarius*, it attains to seven times the length of the body.

The form of the teeth is also constant in a given species, but varies from group to group, and is therefore, when taken in conjunction with their number, of considerable assistance in characterising the divisions of the Gastropoda, especially of the Streptoneura; hence the importance of the radula in systematic works. But occasionally the radula may vary in the individuals of the same species, as, for example, in the Buccinidae; and, on the other hand, groups tolerably far apart from one another may exhibit analogous features in the radular teeth. Further, it has been shown that the number of teeth in a transverse row varies in all the groups founded upon this character. Among the Taenioglossa, in which the radular formula is 2.1.1.1.2, the two marginals are absent in *Lamellaria* and *Jeffreysia*; and contrariwise, there are more than two marginal teeth in certain species of *Turritella*, in *Struthiolaria*, and *Triforis*. A still larger number of teeth, but no median tooth, is found in *Solarium*, *Scalaria*, and *Janthina*. In the Rachiglossa, characterised by the formula 1.1.1, the central tooth is reduced in *Columbella*, and the laterals absent in the Marginellidae and in certain Volutidae and Mitridae, and in the young *Harpa*, the adult in the last-named genus being devoid of a radula. Finally, although the radular formula of the Toxiglossa is given as 1.0.1, there is a central tooth, and more than one lateral in sundry Pleurotomatidae (*Spirotropis*: 1.1.1.1.1). The radula is absent in a few genera only, and those are generally parasitic or suctorial forms, such as *Thyca*, the Eulimidae, Pyramidellidae, Coralliophyllidae, and certain *Terebra* among the Streptoneura, and in the Tornatinidae, *Cymbuliopsis*, *Gleba*, the Doridiidae (in which a vestige of the radular caecum is still retained), the porostomatous Doridomorpha (*Doridopsis*, *Corambe*, Fig. 164, *Phyllidea*), and the Tethyidae.

The buccal opening of Gastropods is furnished with glands, often in considerable quantity (Bullidae, Nudibranchs), and in many stylommatophorous or terrestrial Pulmonates these glands are so highly developed as to form lobulated masses known as the "organs of Semper." But in all Gastropods, with very rare exceptions, the salivary glands proper open into the interior of the buccal cavity on either side of the radula. These organs are generally simple mucous glands, without any digestive action, but in certain forms—*Dolium galea* is an instance—their secretion contains as much as 4 per cent of sulphuric acid, which serves to dissolve the calcareous spicules of the animals taken as food. In the aspidobranchiate Streptoneura and in many other Gastropods the salivary glands are racemose in structure, but in more specialised genera they have the form of more or less elongated tubes (*Janthina*) or of sacs (*Dolium*). In the Aspidobranchs, *Ampullaria*, and the Actaeonidae (Fig. 57) the salivary ducts are very short and open behind the perioesophageal nerve-collar, but the glands traverse the nerve-collar, and their ducts are long and open in front of it in the majority of Gastropods. This is the case in all the Euthyneura—the salivary glands being situated very far back in the Pleurobrancheae—and in the Taenioglossa, with the exception of *Natica*, certain species of *Calyptraea*, etc., in which the ducts are too short to traverse the nerve-collar. Finally, in the Stenoglossa and Heteropoda the salivary glands open in front of, but do not traverse the perioesophageal nerve-collar, their ducts, if they are sufficiently long to reach it, passing outside the structure. In certain forms, *e.g. Fulgur*, *Conus*, many *Terebra*, *Umbrella*, several Pulmonates, etc., the two salivary glands appear to be fused, but retain their individuality. In some siphonate prosbosciferous Taenioglossa, such as *Dolium*, *Cassis*, *Triton*, *Voluta*, and also in *Pleurobranchaea*, the salivary ducts bear a dilatation near their extremities. The two glands exhibit a certain degree of asymmetry in *Strombus*, *Xenophorus*, and some species of *Atlanta*. In several cases there is more than one pair of salivary glands; the Docoglossa possess two pairs, with distinct and separate ducts. In *Janthina* and *Scalaria* there are two pairs of glands, lying close together and appearing to be formed by the bifurcation of a single pair. There are also two separate pairs—the second pair being ventral and anterior to the normal pair—in various Rachiglossa, *Purpura*, *Trophon*, *Voluta*, Cancellariidae, and Haliidae; with the exception of the Muricidae this second pair is anterior to the perioesophageal nerve-collar, and its ducts are often fused in the median line. Many prosbosciferous Opisthobranchs also have more than two salivary glands: in the porostomatous Doridomorpha (*Doridopsis*, Phyllidiidae) the second pair is ventral and anterior, with a single duct; in *Pleurobranchaea* and *Pleurobranchus* there is a third dorsal and median gland.

The buccal cavity is followed by an oesophagus, with plicated walls. This oesophagus is generally long, and often presents dilatations on its course, which may be described under one or any other of the following headings:—(1) A sort of simple pouch with thin walls, as in the Heteropods (Figs. 141 and 142, *m*) and certain Opisthobranchs and Pulmonates, or sometimes a muscular swelling, as in *Murex*, *Amphibola*, *Doris*, etc. (2) In the majority of the Aspidobranchs there are, as in the Chitonidae, paired anterior glandular oesophageal pouches, with papillated internal walls.

These organs also recur in *Littorina*. (3) An unpaired folded dilatation near the middle of the oesophagus is found in various carnivorous Taenioglossa, *e.g.* the Naticidae, Lamellariidae, and Cypraeidae; in the last named it is well developed and has a lamellate internal wall. In the same position in the Cassididae there is a pouch separated from the oesophagus and opening into it by a slit. (4) In all the Taenioglossa, with the exception of *Cancellaria*, the Harpidae, and some species of *Terebra*, an important oesophageal gland, known as the "gland of Leiblein," opens into the middle of the oesophagus. Slightly developed in the Olividae and Fasciolariidae, this organ appears under diverse forms: it is a thick glandular mass in *Murex*, a long caecum with thin walls in *Buccinum*, and in Toxiglossa it forms the so-called "poison gland," whose duct traverses the perioesophageal nerve-collar, as in *Voluta*, and opens into the buccal cavity, giving the whole structure the appearance of a third salivary gland. In *Halia* and *Marginella* this organ forms a siphon opening into the oesophagus by its two extremities. (5) In *Nerita* there is also an unpaired oesophageal gland, and among the Opisthobranchs one finds an azygous dorsal pouch in some Bullomorpha, an oesophageal caecum in the Elysiomorpha, and a long glandular appendage in the Lophocercidae.

The terminal part of the oesophagus sometimes presents modifications which produce an apparent modification of the configuration of the stomach following immediately after. This terminal portion is differentiated to form a gizzard with thick muscular walls and furnished internally with masticatory teeth or plates. The last named are variable in number, and may be simply chitinous and pointed or calcified and flattened. This arrangement is found in a large number of Opisthobranchs, viz. in the majority of Bullomorpha (Fig. 76, *m.p*), including the "Pteropoda Thecosomata" (Fig. 60, *m.p*), in various Aplysiomorpha, and in certain Nudibranchia Tritonomorpha (*Marionia*, *Scyllaea*, *Melibe*). The muscular girdle of this gizzard is also recognisable in a certain number of basommatophorous Pulmonates, viz. *Amphibola*, *Auricula*, and in *Limnaea* it is differentiated to form two globular and symmetrical muscular projections. In consequence of the proximity of the specialised portions of the terminal part of the oesophagus to the stomach, the latter appears, in certain cases, to be divided into several successive portions separated by constrictions, notably in *Aplysia*, and also in *Amphibola* and *Limnaea*, in which the oesophagus exhibits an ampulliform dilatation in front of the gizzard.

The stomach proper consists of a simple enlargement of the digestive canal, and its walls are normally and fairly consistently thin, especially in the Streptoneura. The internal wall of the stomach, however, may frequently be lined by a more or less thick and extensive cuticle, which is generally more fully developed near the origin of the intestine, and may extend into it, as in *Paludina*, *Cyclostoma*, and certain Pulmonates. Sometimes this lining presents a specialisation in the form of a longer or shorter cuticular projection known as the *crystalline style*, which may be lodged in a thick-walled caecum or may project as a rod into the proximal part of the intestine. This structure is found in various Docoglossa, temporarily at least in *Fissurella*, in *Trochus*, in numerous Hydrobiidae such as *Bithynia*, *Lithoglyphus*, *Spekeia*, *Tanganyicia* (Fig. 78, *cr.s*), etc., in the Melaniidae and allied forms such as *Paramelania*, *Nassopsis*, *Typhlobia*, etc., and in *Pteroceras* (Fig. 75, *cr.s*) among the Strombidae. In many cases the stomach is furnished with a caecum, generally pyloric in position and contiguous to the openings of the hepatic ducts. This caecum is coiled in a spiral in many Rhipido-

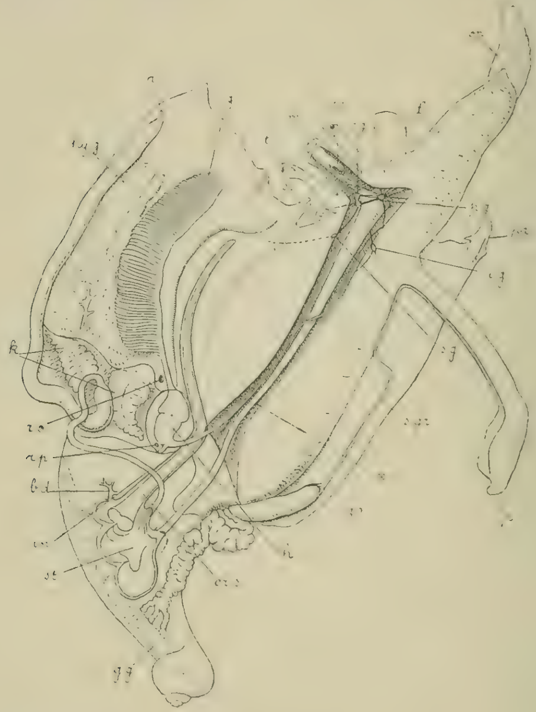


FIG. 75.

Pteroceras, right-side view of the male, with the mantle laid open. *a*, anus; *b.d*, bile-duct; *c.g*, cerebral ganglion; *cr.s*, crystalline style; *f*, foot; *g*, gill; *g.g*, gonad; *g.o*, genital orifice; *h*, heart; *hy.g*, hypobranchial gland; *i.g*, infra-intestinal gland; *in*, intestine; *k*, kidney; *m*, mouth; *oe*, oesophagus; *op*, operculum; *p*, penis; *pa*, mantle; *p.g*, pedal ganglion; *pl.g*, plural ganglion; *ra*, radula; *r.o*, renal orifice; *r.p*, reno-pericardial orifice; *s.g*, supra-intestinal ganglion; *si*, siphon; *s.gr*, seminal groove; *st*, stomach; *t*, tentacle. (After F. M. Woodward.)

glossa, viz. in *Pleurotomaria* (Fig. 127, *sp.c*), *Haliotis*, the Turbinidae, etc., and in *Nassopsis* and *Chytra* (which, according to Moore, possess both the spiral caecum and the style-sac), but is simple and straight in *Ampullaria*, a large number of Opisthobranchia, the Limacinidae, the majority of the Cavoliniidae, *Aplysia*, several Doridomorpha (in which it is rugose internally, and has incorrectly been described as a "pancreas"), and finally in a number of Basommatophora, the Limnaeidae, and various Planorbidae.

The *liver* or digestive gland constitutes the essential organ of digestion. It more or less completely surrounds the stomach, and is divided into lobes, the number and form of which vary in different groups. Primitively there were two lobes, as in other Molluscs, and this number is, as a rule, retained in the Gastropods, but there are very few forms in which the lobes are equal and symmetrical, as in *Neritina* and *Valvata*. More frequently the topographically left lobe is more deeply involved in the spire, and is larger from larval life onwards than the right lobe in dextral Gastropods (Figs. 61 and 116, B); the reverse is the case in sinistral forms. The right lobe may disappear, and the left lobe only persist

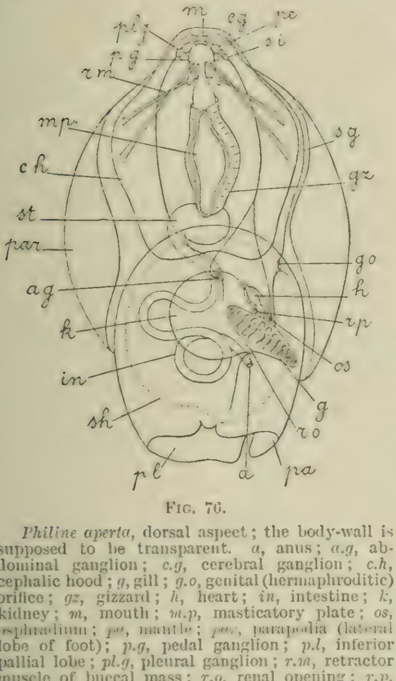


Fig. 76.

Philine aperta, dorsal aspect; the body-wall is supposed to be transparent. *a*, anus; *a.g*, abdominal ganglion; *c.g*, cerebral ganglion; *c.h*, cephalic hood; *g*, gill; *g.o*, genital (hermaphroditic) orifice; *gz*, gizzard; *h*, heart; *in*, intestine; *k*, kidney; *m*, mouth; *m.p*, masticatory plate; *os*, osphradium; *pa*, mantle; *par*, parapodia (lateral lobe of foot); *p.g*, pedal ganglion; *p.l*, inferior pallial lobe; *pl.g*, pleural ganglion; *r.m*, retractor muscle of buccal mass; *r.o*, renal opening; *r.p*, reno-pericardial opening; *s.g*, seminal groove; *sh*, shell; *s.i*, supra-intestinal ganglion; *st*, stomach. (After Guiart.)

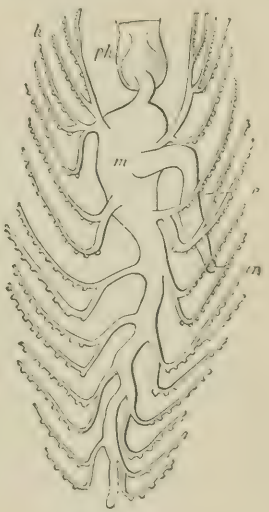


Fig. 77.

Alimentary canal of *Eolis papillosa*, dorsal view. *an*, anus; *c*, hind-gut; *h*, hepatic appendages of the mid-gut (all of which are not figured); *m*, mid-gut; *ph*, pharynx. (From Lankester, after Alder and Hancock.)

in *Paludina* and *Rissoa.* But in *Otina*—a dextral form—it is the left lobe that is the smaller. The liver discharges its secretion into the stomach, but exceptionally it may discharge into the terminal part of the oesophagus or into the intestine (*Philomycus bilineatus*). As a rule there are two hepatic ducts whose openings into the stomach may sometimes be at some distance from one another (*Natica*), but may sometimes be fused as a result of specialisation, as in the majority of the Docoglossa, certain species of *Murex*, and some Euthyneura, viz. the Thecosomata (Fig. 60), *Ancylus fluviatilis*, *Latia*, etc. On the other hand, one of the orifices may be subdivided, so that three hepatic openings are formed, as in the Fissurellidae. In a few rare cases (*Cyclostoma*) isolated acini are found on the hepatic ducts, recalling the condition common in the Cephalopoda. Sometimes the liver lobes cover the whole stomach and open into it by multiple orifices; this arrangement is found in various Opisthobranchs, such as *Gastropteron* and the Gymnosomata. The extreme form of specialisation consists in the subdivision of the whole organ into tubes, which, like the gastric diverticula of Polyclads, extend through the greater part of the body, and even penetrate into external tegumentary appendages. This peculiarity is found in many Nudibranchs, viz. the Eolidomorpha (Fig. 77) and the Elysiomorpha (excepting *Cyerce* and *Lobiancoia*), in which the ramifications of the liver extend into the dorsal papillae, and in various Eolidomorpha communicate with cnidosacs, structures of ectodermic origin which in turn communicate with the exterior (p. 178). A similar arrangement occurs in the Polyclad *Yungia.* The digestive glands secrete a diastatic and peptic ferment, but in addition to their digestive properties they exercise, in the Euthyneura at least, an excretory function, and they also arrest the action of poisonous substances. Lastly, the digestive glands take a share in intestinal absorption.

The *intestine* proper is a cylindrical tube, generally of uniform calibre throughout its course. It is sometimes separated from the stomach by a sort of valve. In nearly all cases it exhibits a well-marked longitudinal projection, the raphe or typhlosole, along a certain part of its course, and in some forms this projection is divided into two in such a manner as to form a groove bounded by two folds. In herbivorous Gastropods, such as *Patella*, the intestine is very long and thrown into coils; in carnivorous forms it is short and often straight as in *Pteroceras* (Fig. 75), *Eolis* (Fig. 77), *Hemifusus* (Fig. 99).

The intestine traverses the ventricle of the heart in most Rhipidoglossa (Fig. 55), the pericardium in *Paludina*, and the substance of the kidney in the *Doliidae*, *Cassididae*, *Triton*, and *Ranella.* In *Murex*, *Purpura*, and the Naticidae the rectal portion of the intestine is provided with a somewhat ramified gland, known as the *anal* *gland*, and in the Fissurellidae there is a longish glandular caecum in the same position, which opens near the anus and lies alongside the rectum as far as the point where the latter traverses the ventricle. As a rule, the anus opens on the right side of the body (on the left side in sinistral forms) and more or less in front. But in those forms in which the coiling of the visceral sac is diminished or lost, this flexure of the digestive canal seems to be effaced and the anus lies at the posterior end of the body. This disposition is rare

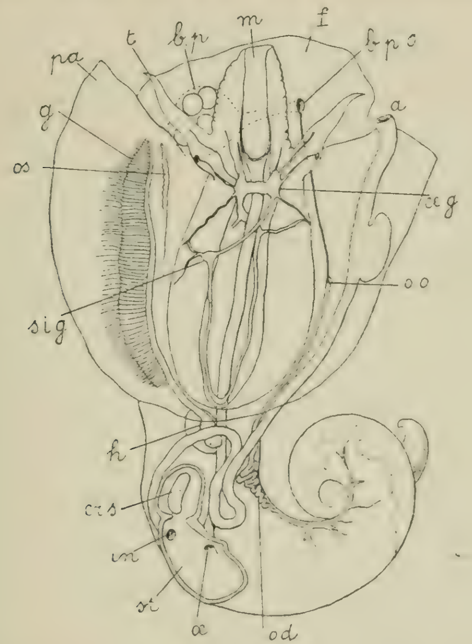


FIG. 78.

Tanganyicia rufilosa, dorsal view, with the mantle laid open. *a*, anus; *b.p*, brood-pouch; *b.p.o*, orifice of brood-pouch; *ce.g*, cerebral ganglion; *cr.s*, crystalline style; *f*, foot; *g*, gill; *h*, heart; *in*, origin of the intestine or pyloric orifice of the stomach; *m*, mouth; *od*, oviduct; *oe*, termination of the oesophagus, or cardiac orifice of the stomach; *o.o*, oviducal orifice; *os*, osphradium; *pa*, mantle; *st*, stomach; *s.i.g*, supra-intestinal ganglion. (After Moore.)

in the Streptoneura, but may be seen in *Cypraea* and *Pterotrachea*. It is, on the contrary, common in the Euthyneura, occurring in *Doridium*, *Runcina*, *Aplysia* (Fig. 154), the Doridomorpha (Fig. 79, VIII), *Janus*, *Alderia*, *Limapontia*, *Testacella*, the Oncidiidae (Fig. 59), and the Vaginulidae (Fig. 87).

2. *The Circulatory System.*—The blood is generally a colourless liquid containing amoebocytes. It is red in the genus *Planorbis* (with the exception of *P. albus*), in which haemoglobin is diffused in the plasma. The muscles of the buccal mass are impregnated

by haemoglobin in a fairly large number of Streptoneura, *e.g.* *Littorina*, *Buccinum*, *Natica*, etc. In some few Gastropods the blood is of a bluish tint in consequence of the presence of an albuminoid containing copper called *haemocyanin*. In other cases the blood is coloured by pigments of extraneous origin absorbed by the amoebocytes; this is the origin of the violet-red colour of the blood of *Fasciolaria*. In various Opisthobranchs, viz. Bullomorpha, Pleurobranchidae, Doridomorpha (Fig. 79, XVII), there is a differentiated lymphatic gland, situated as a rule more or less anterior to the heart on the aorta. In a certain number of Streptoneura this organ consists of a sinus filled with cytogenous connective tissue and situated near the kidney; in other cases it is diffused through the subcutaneous connective tissue.

The heart is always dorsal and in the immediate neighbourhood of the respiratory apparatus (Figs. 79 and 82). It is only in the very archaic forms such as *Pleurotomaria* and the Fissurellidae, that it is still symmetrical and median as in the Cephalopods, Lamellibranchs, and Amphineura, otherwise it is nearly always lateral, being situated on the left in dextral forms (Fig. 67). It is generally somewhat anterior in position (Figs. 82 and 88), but it may become posterior again as a result of secondary specialisation as in *Pterotrachea* (Fig. 143), *Testacella*, *Oncidium*, *Peronia*, and the Doridomorpha, and in the last named it resumes an apparent external symmetry (Fig. 79). The heart of Gastropods always includes an ovoid or piriform ventricle, and in the Rhipidoglossa (with the exception of the Helicinidae, Hydrocenidae, and Proserpinidae) two auricles, but the latter only retain their primitive symmetry in the Fissurellidae, in which the ctenidia themselves retain their symmetry and the heart is median. In other Rhipidoglossa, in which the heart is no longer median, the right auricle is the smaller (Fig. 55, VII), and it becomes more and more rudimentary. In all other Gastropods there is only one auricle, situated on the topographically left side (Fig. 82, *au*): it is generally larger than the ventricle, but its muscular fibres are fewer in number and its walls are thin, transparent, and extensible. The ventricle is traversed by the rectum in the Rhipidoglossa (except the Helicinidae), and in the more archaic forms is placed between the two auricles, *e.g.* in *Pleurotomaria* (Fig. 127, *h*), *Trochus* (Fig. 55, VIII), etc. In the majority of the Streptoneura (Fig. 99, V), in the Pulmonates (Fig. 86, VII), and in some Bullomorpha—*e.g.* *Actaeon*, *Limacina* (Fig. 63), *Clio virgula*, and *Clio acicula*—this ventricle is posterior to the single auricle; in some Opisthobranchs (*Phyllirhoë*, Fig. 161) and Heteropods the auricle and ventricle are on the same transverse line, and in the majority of Opisthobranchs (Figs. 79, III, and 92, I), the Testacellidae, Oncidiidae, Pterotracheidae, and certain Calyptraeidae the ventricle is in front of the auricle. In adult individuals, during normal respiration, the ventricle beats not more than one hundred times nor less than thirty times in a minute.

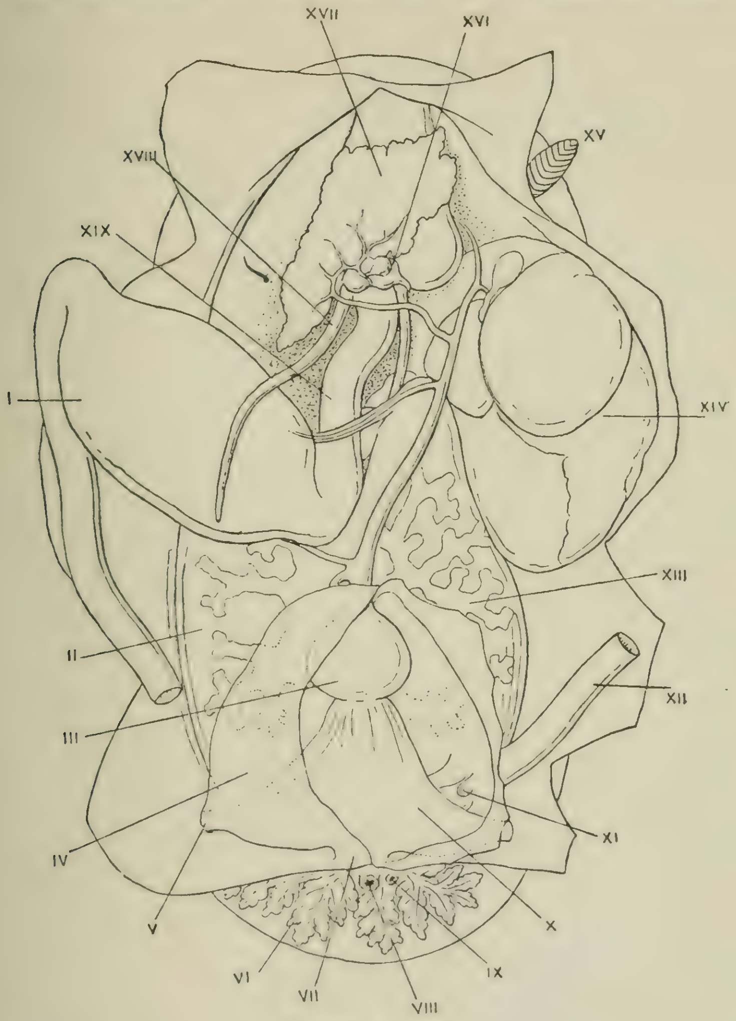


FIG. 79.

Doris pilosa, opened dorsally. I, stomach; II, liver; III, ventricle of heart; IV, pericardium laid open; V, pallial vein; VI, gill; VII, branchial vein; VIII, anus; IX, renal pore; X, auricle; XI, reno-pericardial orifice; XII, posterior part of intestine (the anterior part is on the left); XIII, kidney; XIV, accessory genital glands; XV, tentacle; XVI, central nervous system; XVII, hematic gland; XVIII, salivary gland; XIX, oesophagus. (After Hancock.)

The mean frequency of the pulsations is sixty to the minute in forms most easily observed, such as Pulmonates, Nudibranchs, Bullomorpha, Thecosomata, and Heteropoda. During hibernation the heart of Gastropods does not beat more than twice a minute.

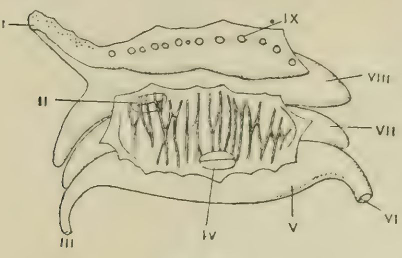


Fig. 80.

Heart of *Patella vulgata*, the auricle and ventricle opened. I, "branchial" vein; II, auriculo-ventricular valve; III, posterior aorta; IV, valve between the ventricle and the aortic bulb; V, aortic bulb; VI, anterior aorta; VII, ventricle, with its internal muscular columns; VIII, auricle; IX, pores leading into the auricle the blood of the roof of the pallial cavity. (After Wegmann.)

The Gastropods in general have a well-developed arterial system, but the venous system is for the most part lacunar. A single artery takes its origin from the end of the ventricle opposite to the auricle—or from the posterior end of the ventricle in diotocardiate Rhipidoglossa—but in the Docoglossa (Fig. 82) one of its branches, namely, the genital artery, appears to have a distinct origin, as in the Cephalopoda. An intra-pericardial aortic bulb is found at the origin of the aorta in *Patella* (Fig. 80, V), various species of *Fissurella*, *Ampullaria*, *Natica*, and the Heteropoda, and a similar but extra-pericardial bulb in *Siphonaria*. In certain Heteropoda, Thecosomata, and Nudibranchs there is a valve at the origin of the aorta. The ramifications of the aorta form an arterial system extending throughout the body, which is continued into a system of interorganic lacunae, without epithelial walls, into which the arterial trunks sometimes open suddenly by contractile orifices; for instance, the cephalic artery of *Patella* and *Haliotis*, the pedal artery of Heteropods, the cephalic artery of Thecosomata, etc. The venous blood is collected from the lacunar system into two large and important sinuses—an anterior or cephalo-pedal sinus and a posterior abdominal or visceral sinus. These two blood-spaces open into an anterior abdominal sinus lying beneath the pericardium. From the last named the blood is carried to the roof of the pallial cavity for oxygenation, on the right side by the rectal sinus (external to the rectum), on the left side by the more or less well-defined lateral sinus which runs along the anterior border of the mantle, and forms the "pulmonary artery" in Pulmonata. Thus the venous section of the circulatory system ends in regular vessels, and in *Aplysia* the great abdominal sinus may be seen to open abruptly, by gaping orifices, into the afferent branchial vessel. The blood is carried from the rectal sinus to the respiratory apparatus by a transverse vessel or by a vascular network which generally forms an afferent branchial sinus running along the whole length of the branchia on the right side. But a very large part of the venous blood, larger in the archaic than in the more specialised forms, passes into the kidney by means of a *portal system*, and the efferent renal vein generally joins the rectal sinus or is carried direct to the afferent branchial sinus (*Valvata*). The venous blood of the kidney is therefore carried to the respiratory organs before it is returned to the heart; but in some Streptoneura (*Vermetus*, *Littorina*, *Cyclostoma*) and in certain Pulmonates the blood is carried direct to the auricle without passing through the respiratory apparatus.

The *respiration* of Gastropods is primitively aquatic and remains so in the majority of forms. The organs of aquatic respiration consist of a pair of leafy expansions of the mantle, situated in the pallial cavity and called ctenidia. Each ctenidium is the homologue of a single branchia of *Chiton* (Fig. 28, B, *g*), of *Nautilus* (Fig. 276), or of *Nucula* (Fig. 206), but most usually only one, namely, that of the topographically left side, persists (Figs. 82 and 85). It is only in the more primitive Rhipidoglossa—viz. the Pleurotomariidae (Fig. 127), the Fissurellidae (Fig. 81), and the Haliotidae—that a pair of ctenidia persists. In the Fissurellidae these two organs are quite symmetrical and of equal importance, but in the Pleurotomariidae and Haliotidae the topographically right ctenidium is smaller than the left, and in all other Gastropods there is only a single ctenidium, that of the right side having completely disappeared. In all the Streptoneura, the Pleurobranchidae, *Gastropteron*, and the Lophocercidae each ctenidium is formed of flattened respiratory filaments which lie parallel to one another and are disposed perpendicularly along one or two faces of a branchial axis. Such a ctenidium is called "pectinate." In the Opisthobranchs—the only Euthyneura that possess ctenidia—the ctenidium is a simple flat and projecting tegumentary lamina, transversely folded from its base to its extremity in such a manner that the ridges of one face correspond to the furrows of the other face: such a branchia is called "plicate."

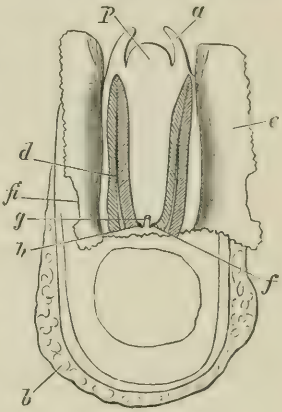


FIG. 81.

Dorsal view of a specimen of *Fissurella* from which the shell has been removed, and the anterior area of the mantle-skirt has been longitudinally slit and its sides reflected. *a*, cephalic tentacle; *b*, foot; *d*, left (archaic right) gill-plume; *e*, reflected mantle-flap; *fi*, the fissure or hole in the mantle-flap traversed by the longitudinal incision; *f*, right (archaic left) renal aperture; *g*, anus; *h*, left (archaic right) renal aperture; *p*, snout. (After Lankester.)

Among the dibranchiate Aspidobranchs, *Pleurotomaria*, the Fissurellidae, and the Haliotidae have two rows of pectinations to each ctenidium, one on either face of the branchial axis (Fig. 81). Each ctendium is therefore formed like that of *Chiton*, *Nautilus*, or

Nucula, and is similarly free to a greater or less extent at its distal extremity. But in *Scissurella* (Fig. 54, IV) the right ctenidium is already degenerate in so far that it has only a single row of filaments inserted directly on the wall of the pallial cavity. The other ctenidiate Aspidobranchs have only a single and equally bipectinate ctenidium, as has also *Valvata* (Fig. 132, *gi*). The two rows of respiratory filaments are equal in the dibranchiate Rhipidoglossa, in the Acmaeidae and Valvatidae, but in the monobranchiate Rhipidoglossa the dorsal row—that is to say, the row between the mantle and the branchial axis—is already much reduced, and in the remainder of the Streptoneura this row of filaments has disappeared, as in the right ctenidium of *Scissurella*, and the single ctenidium is attached to the mantle for the whole of its length (Fig. 99, XVII). The individual branchial filaments are usually simple, but sometimes their surfaces are folded, and again each filament may be in its turn leafy or beset with plications as in the Cephalopoda: this condition is found in *Janthina*. Each filament is a simple tegumentary projection without any internal endothelial lining. The wall of the blood-space contained in it is formed of connective tissue, thickened and compacted along the borders of the filament, where it forms a supporting structure, specially well developed on the ventral side. By these means the rigidity of the filaments, which are often very long as in *Calyptraea*, etc., is ensured. The cavities of the filaments are traversed by muscular trabeculae, by whose agency the whole filament may be contracted.

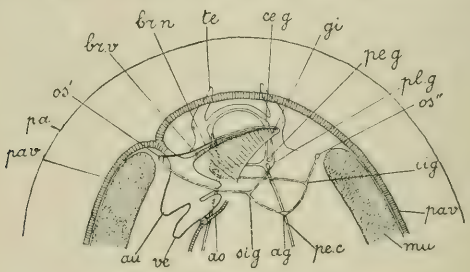


FIG. 82.

Anterior part of the body of *Acmaea*, showing nervous and circulatory systems, dorsal aspect. *a.g*, abdominal ganglion; *ao*, aorta; *au*, auricle; *br.n*, branchial (ctenidial) nerve; *br.v*, branchial vein; *ce.g*, cerebral ganglion; *gi*, gill; *i.i.g*, infra-intestinal ganglion; *mu*, columellar muscle; *os'*, *os''*, left and right osphradia; *pa*, mantle; *pa.v*, pallial vein; *pe.c*, pedal cord; *pe.g*, pedal ganglion; *pl.g*, pleural ganglion; *s.i.g*, supra-intestinal ganglion; *te*, tentacle; *ve*, ventricle.

In spite of the presence of ctenidial branchiae, there is a certain number of Gastropods in which the oxygenated blood returned to the auricle is not derived from these organs alone. A considerable quantity may come from various other parts of the mantle, or, in forms in which the mantle has disappeared as a shell-forming organ, from the dorsal envelope of the body, which in this case serves as an accessory respiratory organ. This phenomenon is to be seen in the Acmaeidae (Fig. 82, *pa.r*), the Heteropoda, the Pleurobranchidae, and the Pneumodermatidae, these last-named families being naked. In the Pleurobranchidae, the Heteropoda, and certain Acmaeidae the mantle is no longer furnished with accessory respiratory structures, but in other Acmaeidae, such as *Scurria*, etc., and certain Pneumodermatidae (Fig. 84, VI, VII), a ctenidium, or branchia properly so called, coexists with secondary respiratory organs or pallial branchiae: these lie below the mantle edge in *Scurria* and on the free surface of the posterior part of the body in the Pneumodermatidae. If the ctenidium is atrophied and disappears altogether, the mantle itself resumes the respiratory function which was previously localised in the ctenidium. This

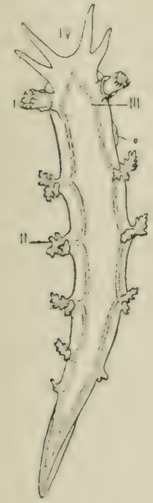


FIG. 83.

Tritonia lineata, dorsal view. I, rhinophore or posterior tentacle; II, dorsal appendage (pallial gill); III, right eye; IV, frontal veil; *o*, genital (hermaphroditic) orifice. (After Hancock.)

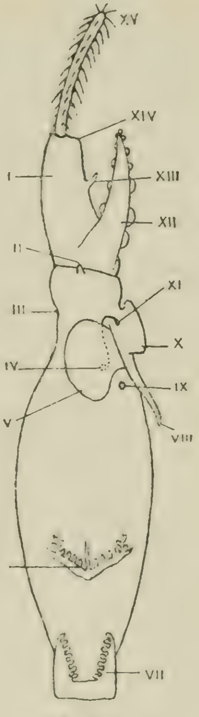


FIG. 84.

Pneumonoderma, right-side view, with the head above. I, the expanded proboscis; II, anterior tentacle; III, posterior tentacle; IV, genital (hermaphroditic) opening; V, right fin; VI, ctenidium; VII, posterior pallial gill; VIII, posterior lobe of the foot; IX, reno-anal cloaca; X, lateral margin of the foot; XI, penial orifice; XII, sucker-bearing appendage; XIII, ventral median papilla of the proboscis; XIV, seat of the mandibles; XV, expanded right hook-sack.

phenomenon may be found both in aquatic species and in forms adapted to terrestrial life, the different modifications of the mantle being as follows:—

(1) There may be branchial structures varying in form and position, but not homologous to a ctenidium. In the Docoglossa these pallial branchiae are situated on the internal face of the mantle, as in *Patella* (Fig. 125, *f*). In various Gymnosomata (*Clionopsis*, *Notobranchaea*, etc.) they are situated on the posterior surface of the body as in the Pneumodermatidae. In the majority of the Nudibranchs they are on the dorsal surface of the body, sometimes localised round the anus as in the Doridomorpha (Fig. 79), sometimes concealed below a fold of the dorsal integument as in *Pleurophyllidia* and certain porostomatous Doridomorpha, *Phyllidia*, and *Corambe* (Fig. 164, *g*). Or all kinds of accessory branchial formations may have disappeared, and the function of respiration is distributed over the whole free surface of the pallial integuments, as may be seen in various Docoglossa such as the Lepetidae and *Bathysciadium*; in *Firoloida* among the Heteropoda; in *Dermatobranchus*, *Heterodoris*, the Elysiomorpha (with the exception of the Hermaeidae), and *Phyllirhoë* (Fig. 161) among the Nudibranchs; in the Clionidae and Halopsychidae (Fig. 156) among the Gymnosomata.

(2) An adaptation to a terrestrial life and the pulmonary respiration resulting therefrom is found in very different groups of Gastropods, but the different stages of evolution are best studied in the Streptoneura. In this group certain aquatic and littoral forms, though they possess ctenidia, have acquired the habit of living for a longer or shorter time beyond the reach of the water. This is the case with various species of *Littorina* (*L. rudis*, *L. neritoides*, etc.), *Cremnoconchus*, *Neritodryas*, several Cerithiidae, etc. Consequently certain modifications of the internal surface of the mantle are induced, in the interior of the pallial or respiratory cavity. The filaments of the ctenidium—bipectinate in *Neritodryas*, but monopectinate in other forms—are often reduced in height and are prolonged more or less indefinitely on the right side of the internal pallial surface to form vascular arborisations, as may be seen in the semi-aerial species of *Littorina* (Fig. 85, *x*) and in *Cremnoconchus*. Finally, the ctenidium disappears altogether, and with it the hypobranchial gland and the efferent branchial sinus, and the venous blood of the rectal sinus is conducted to the afferent cardiac vein (corresponding to the efferent branchial vein) by the system of arborisations that extends over the whole roof of the pallial chamber. Such is the case in *Cerithidea obtusa*, which retains only the vestiges of the anterior extremity of the ctenidium. In many aerial Gastropods the ctenidium has totally disappeared and the roof of the pallial cavity

is permeated by a rich vascular network (Fig. 86) in which the blood is oxygenated. In this manner the respiratory pallial chamber is transformed into a pulmonary cavity or *lung*, whose vascularised surface is irrigated by the blood derived from various parts of the body. The "lung" of Gastropods, then, is not a spongy organ, but a cavity strictly homologous to the pallial cavity.

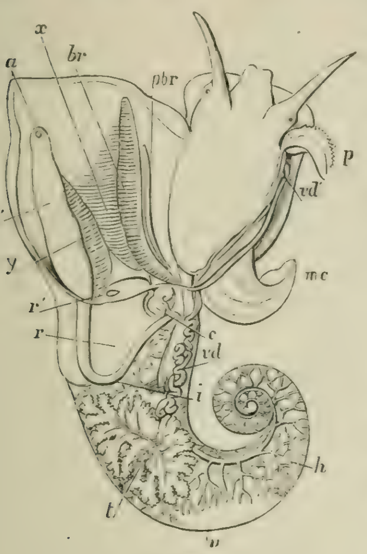


FIG. 85.

Littorina littorea, male, removed from its shell; dorsal aspect; the mantle-skirt cut along its right line of attachment and thrown over to the left side of the animal so as to expose the organs of its inner surface. *a*, anus; *br*, ctenidium; *c*, heart; *h*, liver; *i*, intestine; *m.c*, columellar muscle (muscular process grasping the shell); *p*, penis; *p.br*, osphradium; *r*, kidney; *r'*, aperture of the kidney; *t*, testis; *v*, stomach; *v.d*, vas deferens; *v.d'*, the groove-like part of latter; *x*, vascular prolongations of the ctenidial leaflets; *y*, hypobranchial gland. (From Lankester, after Souleyet.)

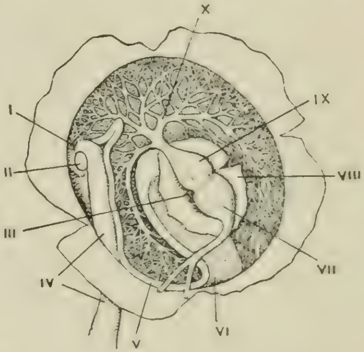


FIG. 86.

Roof of the pallial cavity (lung) of *Limax*. Ventral aspect. I, cloacal (reno-anal) orifice; II, pneumostome; III, reno-pericardial orifice; IV, rectum; V, renal duct; VI, kidney; VII, heart-ventricle; VIII, pericardium (cut open); IX, heart-auricle; X, ramifications of the pulmonary vein. (After Leidy.)

The pulmonate Gastropods exhibiting this structure are polyphyletic, that is to say, they belong to several different groups. Among the Streptoneura we find three families of Rhipidoglossa, viz. the Helicinidae, Proserpinidae, and Hydrocenidae; and three sub-groups of Taenioglossa without probosces, viz. the Cyclophoridae, Cyclostomatidae, and Aciculidae; and among the Euthyneura all the Pulmonates proper, including the aquatic as well as the terrestrial forms. In one family only of the Streptoneura, the Ampullariidae, is the ctenidium preserved at the same time that a pulmonary cavity is present. In this family the pallial cavity is divided by an incomplete septum into a lung and a branchial cavity, the former being situated to the left of the ctenidium. The animal is therefore able to breathe by its gill in the water, and by its lung when out of the water, the air being admitted by a very extensible pallial siphon. In the pulmonate Streptoneura the pulmonary chamber retains the whole of the primitive opening of the pallial cavity; in the Euthyneura, on the contrary, the opening of the lung or pneumostome is much reduced by the fusion of a large extent of the mantle border with the neck of the animal, a fusion that leaves only a minimal but extensible posterior aperture (Fig. 177, V) in the neighbourhood of the anus. This disposition allows of the blood, on its arrival at the lung, being carried round a more or less annular circumpulmonary venous sinus. In the Oncidiidae the lung is somewhat rudimentary, being reduced to arborisations ramifying among the lobes of the kidney. In other Pulmonates such as *Ancylus* and the Vaginulidae (Fig. 87) the reduction of the lung is carried to the point of complete disappearance. Finally, there is a family of Pulmonates in which, instead of a vascularised lung, there is a pulmonary chamber continued into numerous tubules which penetrate into the surrounding blood sinuses: these *tracheate* Pulmonates are the Janellidae (Fig. 90, *tr*). A large number of Pulmonate Gastropods, while preserving their aerial respiration, have returned to an aquatic life; such are the Basommatophora (Limnaeidae, etc.). Among these the marine genera *Amphibola*, *Siphonaria*, and *Gadinia*; *Limnaea abyssicola*, an inhabitant of deep lakes; and *Planorbis nautilus*, have a pallial pulmonary cavity which, instead of being filled with air, may temporarily or continuously be filled with water, as in the larvae of aquatic Pulmonates. Here we see a return and readaptation to aquatic respiration, but for all that the ctenidium does not reappear, a fact which illustrates the irreversibility of evolution. But in these cases respiratory pallial outgrowths or secondary branchiae may be formed near the opening of the pulmonary cavity or even in its interior. Such is the contractile extrapulmonary tegumentary appendage at the base of which the anus opens in *Planorbis* (as this is a sinistral

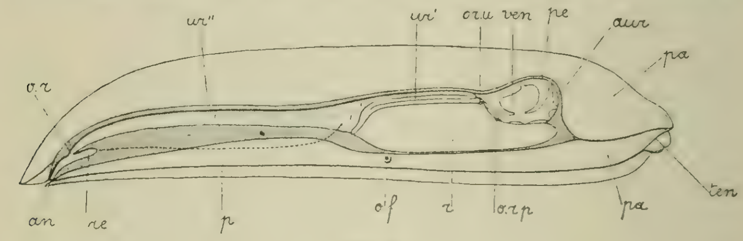


FIG. 87.

Vaginula occidentalis, right-side view, with the mantle partially removed on this side. *an*, anus; *aur*, auricle; *o.f*, female orifice; *o.r*, renal opening in the rectum; *o.r.p*, reno-pericardial pore; *o.r.u*, orifice of the kidney in the ureter; *p*, foot; *pa*, mantle; *pe*, pericardium; *r*, kidney; *re*, rectum (the dotted line shows the direction of the intestine); *ten*, tentacles; *ur'*, *ur''*, primary and secondary ureters; *ven*, ventricle.

genus the appendage is to the left of the pallial aperture). In *Planorbis corneus* (Fig. 89, *g*) there is a single respiratory lobe, with a richly vascularised surface, and in *Ancylus* there is a similar structure, but the lung has disappeared. In *Bulinus*, including the sub-genera *Isidora*, *Pulmobranchia*, etc., and in *Miratesta* there is a folded branchia. In *Siphonaria* the long plicated branchia which extends across the interior of the roof of the pulmonary cavity, between the kidney and the rectum, is of the same character. This branchia is situated more posteriorly and to the right than the ctenidium of monobranchiate Gastropods (Fig. 174). The diverse characters of the respiratory apparatus of Gastropoda may be advantageously summed up in the following table :—

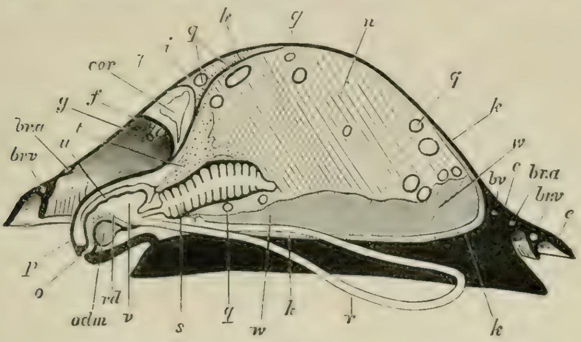


FIG. 88.

Diagram of a sagittal section of *Patella vulgata*. *br.a*, branchial afferent vessel (artery); *br.v*, branchial efferent vessel (vein); *b.v*, blood-vessel; *c*, muscular substance forming the root of the foot; *cor*, heart within the pericardium; *e*, mantle-skirt; *f*, papilla of the larger kidney; *g*, anus; *i*, smaller kidney; *k*, larger kidney; *l*, pericardium; *n*, liver; *o*, mouth; *od.m*, muscles and cartilage of the odontophore; *p*, snout; *q*, intestine in transverse section; *r*, radular or lingual sac; *rd*, radula; *s*, lamellated stomach; *t*, salivary gland; *u*, duct of same; *v*, buccal cavity; *w*, gonad. (After Lankester.)

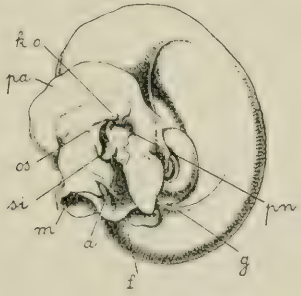


FIG. 89.

Planorbis corneus, removed from the shell; anterior view. *a*, anus; *f*, foot; *g*, gill; *k.o*, renal aperture; *m*, mouth; *os*, osphradium; *pa*, mantle; *pn*, pneumostome; *si*, pulmonary siphon.

Ctenidial breathing	bictenidial	with 2 bipectinate ctenidia		with 2 symmetrical ctenidia	Fissurellidae.
				with left ctenidium greater	*Pleurotomaria* and Haliotidae.
		with right ctenidium monopectinate			*Scissurella*.
	monoctenidial, with gill	pectinated	bipectinate	with 2 equal pectinations	*Valvata*.
				with ventral pectination larger	Rhipidoglossa.
			monopectinate		Pectinibranchia generally.
		wrinkled			Tectibranchia generally.
Ctenidial and pallial breathing	without accessory gill				Pleurobranchidae and some Acmaeidae.
	with accessory gill				Acmaeidae and Pneumonodermatidae.
	with a lung				*Ampullaria*.
Pallial breathing	true aquatic			without accessory gill	Lepetidae, Elysiomorpha, *Phyllirhoë*, *Firoloida*, *Clione*, *Halopsyche*.
				with accessory gills	Patellidae, Nudibranchia, *Clionopsis*, *Notobranchaea*.
	exclusively by a lung			with aerial lung	Pulmonata, Helicinidae, Hydrocenidae, Proserpinidae, Cyclophoridae, Cyclostomatidae, Aciculidae, *Geomelania*.
				with aquatic lung	*Amphibola*, *Gadinia*, *Chilina*, *Limnaea abyssicola*, *Planorbis nautileus*.
	tegumentary (no lung)				*Vaginula*.
	with a lung and an			intrapulmonary accessory gill	*Siphonaria*.
				extrapulmonary accessory gill	*Planorbis corneus*, *Bulinus*, *Miratesta*.
	with accessory gill and without lung				*Ancylus*.

3. *Excretory Organs.*—In the Gastropoda the kidneys are the essential organs of excretion, but the pericardial glands serve as accessory excretory organs, as also certain parts of the body in which the products of excretion are collected, forming veritable accumulative kidneys.

(1) The kidneys are originally paired, as in all other Mollusca, and a single pair is found (Figs. 55, III, XIII; 81, *f*, *h*; 91, 127) in all the Aspidobranchia, except the Neritacea, including the Neritidae and allied families. These two kidneys open one on each side of the anus, but they do not retain their primitive symmetry in any Gastropod, and although they are independent of one another, the topographically left kidney is rudimentary, and that of the right side alone is functional in almost every case.

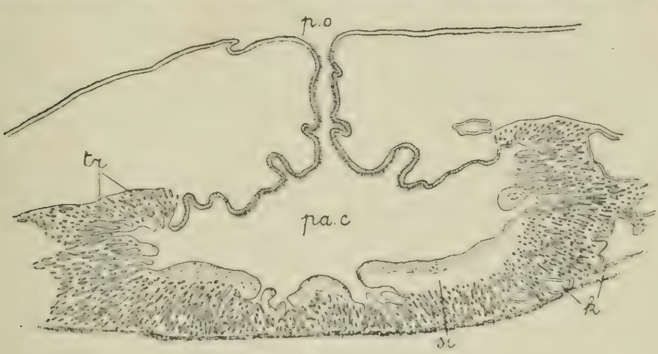


Fig. 90.

Transverse section of the lung of *Janella*. *k*, ureter; *pa.c*, pallial or pulmonary cavity; *po*, pneumostome; *si*, blood sinus; *tr*, "tracheae" or diverticula of the pulmonary cavity. (After Plate.)

In the Neritacea (Neritidae, Titiscaniidae, Helicinidae, Hydrocenidae, and Proserpinidae) and in all the Pectinibranchia and Euthyneura the topographically right kidney no longer exists. In *Paludina* the two kidneys coexist during development, but in the adult that of the topographical right side has disappeared. As regards the position of these organs, their primitive situation is wholly within the visceral mass (Docoglossa, Fig. 88, *k*), and their migration outside the visceral mass is a specialisation which begins to show itself in the Rhipidoglossa—at any rate, in the case of the left kidney (Fig. 127)—and is completely realised in the case of the single kidney in other Streptoneura and Tectibranchia, in which the excretory organ is more and more localised in the mantle (Figs. 75, *k*; 63, *r*). The kidney is always a dorsal organ, situated in the neighbourhood of the pericardium, with which it communicates by a ciliated aperture. In the detorted Aspidobranchs (Fissurellidae), however, the very rudimentary left kidney has lost this pericardial communication. *Elysia* is exceptional in that the kidney is placed below and partly surrounds the pericardium, and the reno-pericardial orifices are multiple, some ten being present (Fig. 92). As a rule the external opening of the kidney is situated near the anus (Figs. 81 and 88), and sometimes the two open together into a sort of common cloaca, as may be seen in the Gymnosomata (Fig. 84, IX) and in certain Pulmonates, such as *Limax* (Fig. 86, I), the Onciidiae (Fig. 59), and *Vaginula* (Fig. 87), but not in *V. willeyi*. In rare cases, however, such as the Nudibranch *Janus*, the excretory aperture is distant from the anus. The external renal orifice is borne on a papilla in various Aspidobranchs with two kidneys (Fig. 88, *f*), but is a simple slit, shaped like a button-hole, in the majority of Pectinibranchia (Fig. 99, IV) and Tectibranchia (Fig. 154, *o*). Among the Pectinibranchs, however, *Paludina* and *Valvata* are exceptional in possessing an ureter which opens at the edge of the mantle. The same arrangement is found in many Pulmonata, especially in the Stylommatophora, in which an elongated ureter opens alongside of the anus at the margin of the pneumostome (Fig. 86, V).

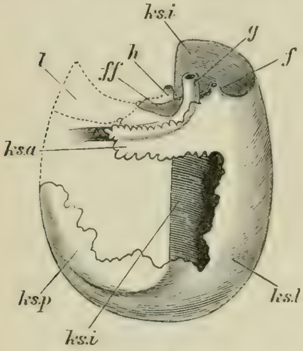


Fig. 91.

Diagram of the two renal organs of *Patella*, to show their relations to the rectum and to the pericardium. *f*, papilla of the larger kidney; *g*, anal papilla, with rectum leading from it; *h*, papilla of the smaller kidney, which is only represented by dotted outlines; *l*, pericardium, indicated by a dotted outline (at its right side are seen the two reno-pericardial pores); *ff*, the sub-anal tract of the large kidney given off near its papilla and seen through the unshaded smaller kidney; *ks.a*, anterior superior lobe of the large kidney; *ks.l*, left lobe of same; *ks.i*, inferior sub-visceral lobe of same; *ks.p*, posterior lobe of the right kidney. (After Lankester.)

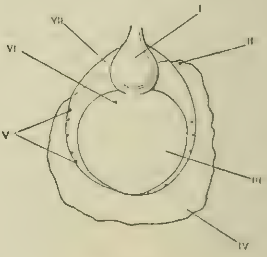


Fig. 92.

Elysia viridis, heart and kidney, dorsal aspect (somewhat schematic). I, ventricle of heart; II, external renal pore; III, auricle; IV, kidney; V, the various reno-pericardial pores on the left side (there are five such pores on the right-hand side); VI, the ventral reno-pericardial pore; VII, pericardium.

As regards its structure, the kidney in its simplest form is a sac lined by a secretory epithelium. By the infolding of its walls, the cavity of the sac is subdivided and the organ acquires an alveolar structure of spongy appearance, but in various pelagic forms it again becomes more or less tubular and transparent, *e.g.* in the Heteropoda (Fig. 141, *q*), in certain "Pteropoda" (Fig. 60, *k*), in *Phyllirhoë* (Fig. 161, *l*). As a rule the kidney is a compact mass, without external projections, but it is divided into two lobes in Stenoglossa in general and also in some Taenioglossa, viz. *Paludina* and *Cypraea*. In a fairly large number of Nudibranchs (Doridomorpha, *Janus*, etc.) the kidney is divided into ramifications which extend between the visceral organs of the greater part of the body (Fig. 79, XIII). In sundry Pectinibranchs—*e.g.* *Littorina*—there is a "nephric gland" which opens into the kidney, and consists of ciliated canals surrounded by conjunctive tissue. In addition to its excretory function the kidney may also serve for the conduction of the genital products. Thus in all Gastropoda with two kidneys, that is to say, in all the Aspidobranchia (*Pleurotomaria*, *Trochus*, Fig. 55, Fissurellidae, etc.) except the Neritacea, the gonad opens into the right kidney by a papilla situated near the external renal aperture.

(2) The pericardial glands in the Aspidobranchs and *Valvata* are placed on the external walls of the auricles. In other forms they are localised on the internal wall of the pericardium, as in *Littorina* and *Cyclostoma* among the Pectinibranchs and in the Pleurobranchidae and Nudibranchia among the Opisthobranchs, or they are situated within the pericardium on the origin of the aorta, as in Aplysiidae.

(3) Various excretory products may be accumulated in plasmatic cells (known as the "cells of Leydig") in the conjunctive tissue of different parts of the body. This phenomenon is particularly common on the walls of arterial trunks, and may be seen in the caudal artery of *Carinaria*, and on the wall of the arterial trunks of certain Streptoneura and many terrestrial Pulmonates, in which calcareous concretions are found in the perivascular conjunctive tissue. The different forms of excretory apparatus and the special function of each can be revealed by the method of physiological injections.

4. *Nervous System.*—With the exception of the endoparasitic Entoconchidae, all Gastropods possess a well-developed nervous system in which the same cerebral, pedal, pleural, visceral, and stomato-gastric nerve-centres, and the same connectives and commissures, are to be found as in other Molluscs. But the special character of the Gastropod nervous system is the asymmetry of the visceral centres and of the nerves arising from them, an asymmetry resulting from that of the visceral organs themselves. The most primitive form of nervous system is characterised, as in the Polyplacophora, by the absence of concentration in the ganglia. The cerebral centres in the Rhipidoglossa are situated at the sides of the oesophagus and are united by a long commissure which is itself ganglionated (Fig. 94). The pedal centres in Aspidobranchs (Fig. 94, *pe.c*), *Paludina*, and some other taenioglossate Pectinibranchs

such as *Cyclophorus* and *Cypraea*, have the form of long ganglionated cords with multiple commissures or anastomoses. The pleural ganglia are but slightly differentiated in *Pleurotomaria*, in which genus they are placed on the dorsal pedal connective, at a nearly equal distance from the cerebral and pedal centres (Fig. 94, *pl.c*). In forms in which they are better developed, the pleural ganglia are still in intimate contact with the anterior part of the pedal centres, and there are two long connectives, the cerebro-pleural and the cerebro-pedal, on either side of the digestive tube, the pleuro-pedal connective being, on the contrary, very short. This arrangement is known as the "hypoathroid," and is found in Aspidobranchia (Fig. 93) and several Taenioglossa, viz. *Ampullaria*, *Cyclophorus*, and *Nassopsis*. As a result of specialisation we get the "dystenoid" condition, in which the cerebral centres are approximated and the pleural ganglia are shifted nearer to the cerebrals, so that the pleuro-pedal connectives are elongated (Fig. 123, A). Finally, in the "epiathroid" condition, the pleural centres are either in contact or are fused with the cerebrals (Fig. 123, B), as is the case in the

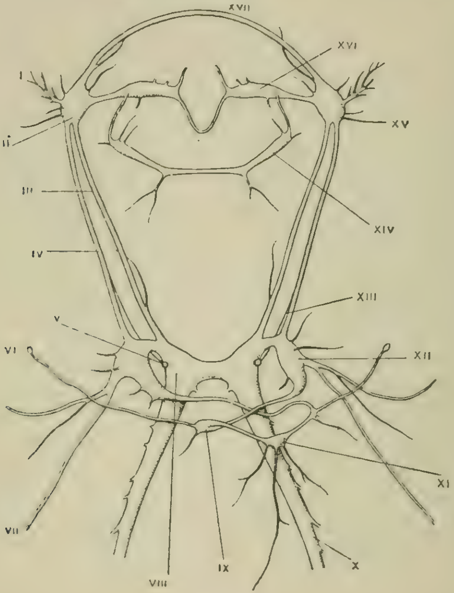


FIG. 93.

Central nervous system of *Patella vulgata*, dorsal aspect. I, tentacular nerve; II, left cerebral ganglion; III, cerebro-pedal connective; IV, cerebro-pleural connective; V, left otocyst; VI, left osphradium; VII, pallial nerve; VIII, anterior part of the pedal cord; IX, supra-intestinal ganglion; X, pedal cords (their posterior endings are not drawn); XI, abdominal ganglion; XII, pleural ganglion; XIII, otocystic nerve; XIV, stomato-gastric ganglion; XV, optic nerve; XVI, labial commissure; XVII, cerebral commissure.

majority of the Pectinibranchia, including the Heteropoda, and in various Bullomorpha (*e.g. Actaeon*, Fig. 57) and the thecosomatous "Pteropods" among the Opisthobranchia. At the same time the pedal ganglia are concentrated anteriorly to form more or less globular masses (Fig. 123, C, *pe.g*).

Primitively the visceral commissure is somewhat extensive, and its ganglionic centres are tolerably far removed from one another, as may be seen in all the Streptoneura and the less specialised Euthyneura (Figs. 94, 57, etc.). These ganglionic centres are normally three in number: one is median, and is called the abdominal or the visceral ganglion proper (Fig. 93, XI); two are lateral, placed right and left on corresponding sides of the visceral commissure. The ganglion on the morphologically left side may be but slightly developed or may not be differentiated at all, as, for example, in monobranchiate Rhipidoglossa. In consequence of the torsion of the visceral mass of Gastropoda, the visceral commissure is normally twisted into a figure of eight; that is to say, the right moiety with the visceral ganglion is situated above the alimentary tract and is displaced to the left, the left moiety remains below the alimentary tract, but is inclined to the right (Fig. 57). Hence the names *supra-intestinal* and *infra-intestinal* are respectively given to the two moieties and to the ganglia borne on them (Fig. 123).

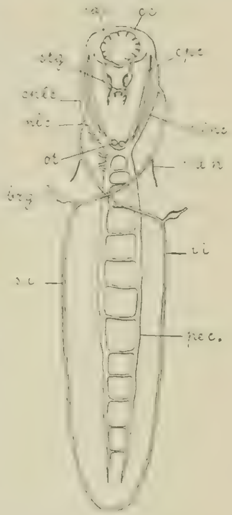


FIG. 94.

Pleurotomaria, nervous system, dorsal aspect. *br.g*, branchial ganglion; *c.c*, cerebral commissure; *c.p.c*, cerebro-pedal commissure; *c.pl.c*, cerebro-pleural commissure; *i.i*, infra-intestinal portion of the visceral commissure; *la.c* labial commissure; *ot*, otocyst; *pa.n*, pallial nerve; *pe.c*, pedal cord; *pl.c*, pleural centre; *pl.p.c*, pleuro-pedal connective; *s.i*, supra-intestinal part of the visceral commissure; *st.g*, stomato-gastric ganglion. (After F. M. Woodward.)

This disposition of the visceral commissure is common to all the Streptoneura (as the name of the group signifies), including the Heteropoda and all the forms formerly called "Orthoneura," *i.e.* forms in which the visceral loop was believed to have never been twisted; it may also be clearly seen in the more archaic Euthyneura (which, as has been explained above, are detorted Gastropods), for instance, in various Bullomorpha (*Actaeon*, Fig. 57, *Scaphander*, *Bulla*, etc.), and in *Chilina*. But in the three last-named genera the detorsion of the visceral commissure is already manifest, that is to say, its supra-intestinal moiety shows a tendency to return to the lower side of the alimentary tract, and its sub-intestinal moiety tends to return to the left side. This detorsion of the visceral commissure is complete in the rest of the Euthyneura, as may be seen in the Opisthobranchia (Figs. 95 and 159) and the Pulmonata (Figs. 96 and 97).

Further, in all the Euthyneura but those which are the most primitive from this point of view, such as the Bullomorpha and *Aplysia* among the Opisthobranchs, the Auriculidae, *Chilina*, and *Latia* among the Pulmonata, there is a tendency to the approximation of the ganglionic centres and at the same time a shortening of the visceral commissure. This is carried so far that the ganglia come into contact and form a chain of several united nerve-centres between the pleural ganglia (Fig. 97). When it has reached this stage of evolution the whole nervous system is concentrated in the cephalic region round the anterior part of the oesophagus, and finally all the ganglia—cerebral, pleural, pedal, and visceral—are intimately united and localised on the dorsal surface of the oesophagus, a condition which may be seen in *Pleurobranchus* and

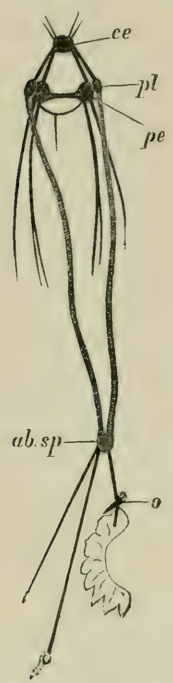


FIG. 95.

Nervous system of *Aplysia* (dorsal aspect), as a type of the long-looped Euthyneurous condition. The untwisted visceral loop is lightly shaded. *ab.sp*, visceral ganglion which represents the abdominal + the supra-intestinal ganglia of Streptoneura, and gives off the nerve to the osphradium and another to an unlettered so-called "genital" ganglion; *ce*, cerebral ganglion; *o*, osphradium; *pe*, pedal ganglion and double pedal commissure; *pl*, pleural ganglion (the stomatogastric commissure and ganglia are omitted). (From Lankester, after Spengel.)

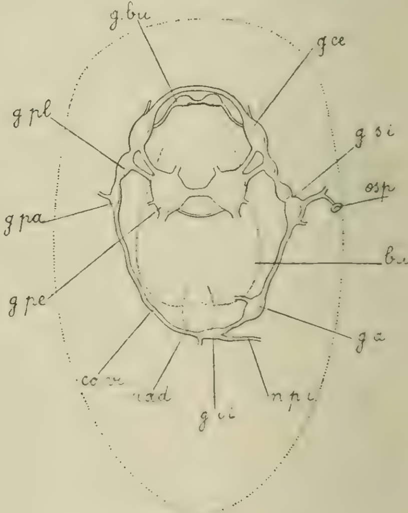


FIG. 96.

Latia neritoides, central nervous system, dorsal view (the buccal mass is indicated by a dotted line). *bu*, buccal mass; *co.vi*, visceral commissure; *g.a*, abdominal ganglion; *g.bu*, buccal ganglion; *g.ce*, cerebral ganglion; *g.i.i*, infra-intestinal ganglion; *g.pa*, parietal ganglion; *g.pe*, pedal ganglion and double pedal commissure; *g.pl*, pleural ganglion; *g.s.i*, supra-intestinal ganglion; *n.p.i*, nerve of the inferior pallial lobe; *osp*, osphradium; *rad*, radula.

the majority of the Nudibranchs (Fig. 159), and is pushed to an extreme in *Tethys.* In this case the pedal and visceral commissures are destitute of ganglia or nearly so on the ventral part of their course. It is only in the thecosomatous "Pteropods" that the concentration of the ganglia takes place ventrad of the oesophagus, the dorsal part of the nervous system being formed only by a long cerebral commissure (Fig. 60, *n.s*).

In all Gastropoda there is an infra-oesophageal stomato-gastric commissure. In the more primitive forms (Aspidobranchia, Fig. 94) the stomatogastric system originates from a sub-oesophageal labial commissure, but in other Gastropods from the cerebral ganglia. Normally this stomato-gastric commissure bears a pair of ganglia situated below the radular caecum at the point of origin of the oesophagus from the buccal bulb (Fig. 146, *g.bu*).

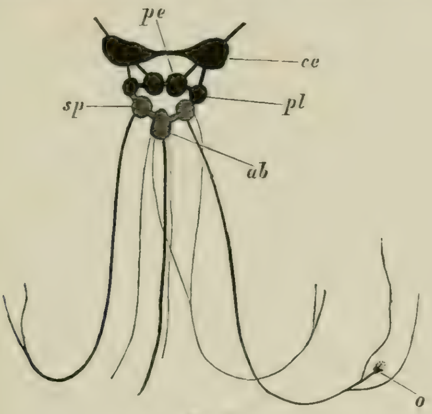


FIG. 97.

Nervous system of *Limnaea stagnalis* (dorsal aspect), as a type of the short-looped Euthyneurous condition. The short visceral loop, with its three ganglia, is lightly shaded. *ab*, abdominal ganglion (+infra-intestinal); *ce*, cerebral ganglion; *o*, osphradium; *pe*, pedal ganglion; *pl*, pleural ganglion; *sp*, parietal ganglion or left visceral ganglion; opposite to it is the visceral ganglion of the right side, or supra-intestinal ganglion, which gives off the long nerve to the osphradium (in *Planorbis*, the osphradium and supra-intestinal ganglion are on the *left* side). (From Lankester, after Spengel.)

As regards the innervation of the different organs, the cerebral centres supply the head and buccal lips, the tentacles and other cephalic appendages, the eyes and the otocysts. The pedal ganglia send out nerves to the whole mass of the foot, including the epipodium, and to a portion of the cervical region. The mantle and the organs connected with it are primitively—as in the Streptoneura—almost entirely innervated from the pleural centres, but they are also partially innervated by nerves which issue from the visceral commissure and the supra- and infra-intestinal ganglia, and pass to the ctenidia and osphradia. The last-named nerve-centres take a preponderant share in the innervation of the mantle in Euthyneura.

especially in the Pulmonata, in which group the pleural ganglia scarcely ever give off any nerves. In all the Euthyneura except *Actaeon* (Fig. 57), *Chilina*, and *Latia* (Fig. 96) the infra-intestinal ganglion is fused with the abdominal (Fig. 97, *ab*) in such a manner that the latter appears to participate in the innervation of the mantle—for instance, in the innervation of the inferior pallial lobe and the pallial branchia of the Planorbidae—and the pallial nerves issuing from the left moiety of the visceral commissure originate from a special and newly-developed ganglion, viz. the parietal ganglion of the Pulmonata (Figs. 96, *g.pa*; 97, *sp*). As regards the viscera, the heart, the kidneys, and the gonad receive their essential nerve supply from the abdominal ganglion, the alimentary canal receives its nerves from the stomato-gastric centres, and these latter nerves sometimes exhibit accessory ganglia on specialised parts of the alimentary tract, such as the gizzard of Tectibranchia, etc.

5. *Sense Organs.*—In addition to sensory cells scattered over the whole surface of the body, Gastropods possess special sensory organs usually designated by the names rhinophore, osphradium, otocyst, and eye. While the whole surface of the integument is sensitive, tactile sensibility is more particularly localised in the anterior regions of the body: in the head, in the margin of the foot (in marine Streptoneura the whole ventral surface of the foot exhibits a fine nervous network), and in the regions of the body specialised to form tactile appendages of various shape and situation. Such are the cephalic tentacles—especially the anterior pair in quadritentaculate Euthyneura; the labial palps (Fig. 117, te'''), which bear a row of tubercles in some Pulmonates; the pedal tentacles of *Vermetus* (Fig. 45, *p.t*); the epipodial tentacles of the Rhipidoglossa (Fig. 130, XI), which have ciliated sensory organs at their bases; and the pallial appendages, such as the dorsal papillae of the Nudibranchs.

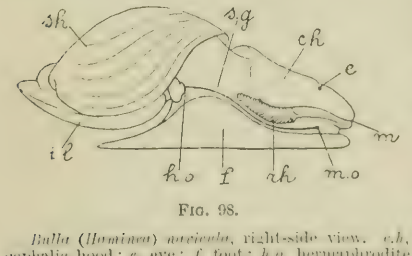


FIG. 98.

Bulla (*Haminea*) *navicula*, right-side view. *c.h*, cephalic hood; *e*, eye; *f*, foot; *h.o*, hermaphrodite orifice; *i.l*, inferior pallial lobe; *m*, mouth; *m.o*, male orifice; *rh*, rhinophore (Hancock's organ); *s.g*, seminal groove; *sh*, shell. (After Guiart.)

The *Rhinophores*, or olfactory organs, as they are called, are likewise constituted by the cephalic tentacles, especially by the posterior pair in the quadritentaculate Euthyneura. The whole surface of these tentacles is covered by little ciliated papillae, giving them a silky appearance, in many Rhipidoglossa, *e.g. Scissurella*, *Haliotis*, *Trochus*, *Gena*, *Molleria*, *Cyclostrema*, *Neritina*, in *Caecum* (Fig. 68, *te*), etc. The olfactory nerve divides into many ramifications which end on the surface of the tentacle in olfactory sensorial cells. In many forms, such as the terrestrial Pulmonata, the majority of the naked Opisthobranchia, *Cyclostrema*, *Xenophorus*, and all the Gastropods without an osphradium, these ramifications issue from a rhinophoric ganglion situated at the extremity of the olfactory nerve. The olfactory end-cells are frequently localised in a tract of higher epithelium at the extremity of the tentacle, or in a furrow excavated in the surface of the tentacle (Pyramidellidae, Fig. 137, *te*, *Solarium*), and in many Opisthobranchia the sensitive surface of this olfactory prominence or cavity is increased by the development of numerous parallel pleats or foliations (Fig. 163, *t*). In terrestrial Pulmonates—*e.g. Helix*—the sense of smell does not extend for a greater distance than half a metre, and then only in the case of exceptional odours; the most usual distance at which odours are recognised is from one to three centimetres, but certain carnivorous marine Streptoneura—for example, *Nassa*—are able to recognise odours at a distance of more than two metres.

The *Osphradia* are the sensory organs of the pallial or respiratory cavity, and exist in diverse forms. There is a pair of osphradia in all the bictenidiate Aspidobranchia and in the Docoglossa: in all other Gastropods the osphradium is unpaired. It disappears only in some terrestrial Streptoneura (Helicinidae and Cyclophoridae), in the Pleurobranchidae, the Nudibranchia, and all the Stylommatophorous or terrestrial Pulmonates; nevertheless in all the stylommatophora (*Limax*, *Helix*, etc.) the osphradium is present during development and during the first few days after hatching. To sum up, then, the osphradium is absent in aerial species or in aquatic forms devoid of a respiratory cavity, and when it is absent a rhinophoric ganglion is present. An osphradium consists of a specialised and usually elevated and ciliated region of the epithelium, in which there is an accumulation of sensory cells. In the ctenidiate Gastropods the organ is situated on the outer side of the ctenidium (Fig. 99, XVI). The most simple form of osphradium is seen in the Streptoneura, in which it is not differentiated into a definite organ, but is merely a localisation of neuro-epithelial cells on the course of the branchial nerve along the two supporting margins of the ctenidia, as in the Fissurellidae, or on an osphradial nerve running along the support and formed by a differentiation of the branchial nerve, as in other Rhipidoglossa, or again on a ganglion placed on the extremity of this special nerve at the base of the ctenidium. In other Gastropods the osphradium becomes a distinct terminal organ at the base or at the left (external) side of the single ctenidium, athwart the current of water which supplies the latter organ. The osphradium may persist in this place after the disappearance of the ctenidium, but only in aquatic forms such as the Patellidae, Gymnosomata, and basommatophorous Pulmonates. In the most archaic Taenioglossa, viz. *Paludina*, *Littorina* (Fig. 85, *p.br*), *Cyclostoma*, *Vermetus*, the osphradium is a filiform epithelial ridge, overlying a nerve or ganglionated cord. Then, as a result of specialisation and multiplication of its surface, the two sides of the ridge become garnished with pectinations, so that the organ acquires a deceptive resemblance to a branchia. This condition may be seen in the more specialised Taenioglossa, such as *Natica*, *Cerithium*, and the Strombidae, in which the pectinations themselves are arborescent; in *Cypraea*, in which the organ is trifid; and in the Rachiglossa (Fig. 99, XVI) and Toxiglossa. In the Euthyneura the osphradium is a simple epithelial projection of circular or elongated shape, lying above an osphradial ganglion, into which it is sometimes invaginated—viz. in certain basommatophorous Pulmonates—and the invagination is bifurcated in *Limnaea*. In the last-named genus the osphradium is situated in the pallial cavity, to the left of the ctenidium; in the Basommatophora it is close to the pneumostome; in *Siphonaria* (in which the lung is filled with water)

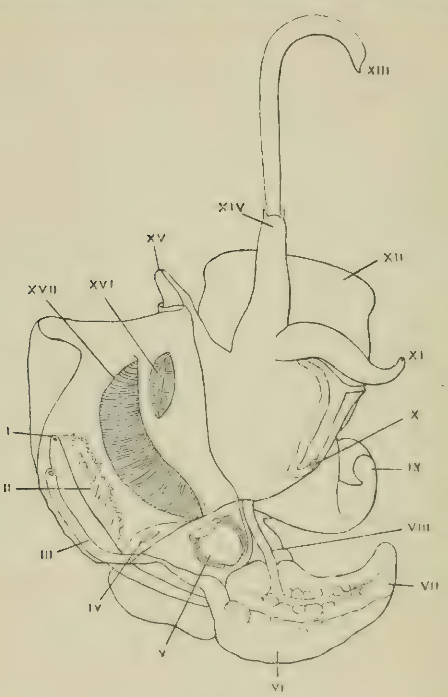


FIG. 99.

A male *Hemifusus tuba*, removed from its shell and with the pallial cavity opened. I anus; II, hypobranchial gland; III, spermiduct; IV, renal pore; V, heart, in the opened pericardium; VI, testis; VII, liver; VIII, oesophagus; IX, columellar muscle; X, the spermiduct cut through, with the mantle; XI, penis; XII, foot; XIII, proboscis; XIV, head; XV, pallial siphon; XVI, osphradium; XVII, ctenidium. (After Souleyet.)

it is inside the pulmonary cavity (Fig. 174); in other forms with an aerial lung it is external (Fig. 89, *os*).

Cyathiform bodies or gustatory bulbs, formed of taste-cells, are found on the lateral and ventral surfaces of the buccal cavity in sundry Rhipidoglossa, and at the sides of the buccal aperture in some Heteropoda. Analogous bodies have been found on the epipodial tentacles of Rhipidoglossa.

The *Otocysts*, or statocysts, are hollow spherical vesicles, whose internal walls are lined by a ciliated epithelium containing sense-cells. These vesicles contain a liquid secreted by their epithelial walls, and in this liquid are calcareous auditory concretions of crystalline structure. There is a single large and spherical concretion or otolith in the more specialised Tectinibranchs and in a few adult Opisthobranchs (*Lobiger*, the Elysiomorpha, Hedylidae, *Pseudovermis*, *Fiona*, and sundry Eolidomorpha), (viz. the Tergipedinidae, *Capellinia*, *Eolidiella*, *Eolis aurantiaca* and *E. olivacea*, *Galvina picta* and *G. exigua*). There are numerous and usually ovoid and elongated concretions, called *Otoconia*, in the Aspidobranchia (except *Bathysciadium*), in some of the less specialised Taenioglossa, such as *Paludina*, *Ampullaria*, *Cyclophorus*, *Valvata*, *Nassopsis*, and the majority of the Melaniidae, and in the Euthyneura in general, with the exception of the Opisthobranchs mentioned above. Otoconia sometimes coexist with an otolith in certain Cerithiidae, *Turritella*, *Doto*, and *Oncidium*, but in all larvae there is only a single otolith (Fig. 116, A, III). Otocysts are absent in the adult *Vermetus* and in some *Janthina*. In creeping Gastropods the otoliths are situated in the foot, in the neighbourhood of the pedal ganglia (Fig. 93, V), and are often adherent to these nerve-centres. In swimming Gastropods, such as Heteropoda, *Phyllirhoë*, and *Glaucus*, they show a tendency to approach the cerebral centres, and the same tendency may be seen in the majority of Nudibranchs. In all cases the otocysts are innervated from the cerebral ganglion, as may be most clearly seen when they are at some distance from the pedal ganglia (Figs. 123, C, *ot*; 142, *u*; 146, *ot*). The neuro-epithelial elements are concentrated in a *macula acustica*, placed opposite the expansion of the otocystic nerve, in the otocyst of Heteropoda.

Cephalic eyes exist in almost all Gastropods, and there are, in addition, pallial eyes in certain Oncidiidae. The two cephalic eyes are situated on the tentacles, in the Euthyneura on the posterior pair of tentacles. In the Streptoneura these eyes are placed at the outer side of the base of each tentacle, and are borne on tubercles (Fig. 44, A, *e*) which may fuse with the tentacles, and thus, in a number of instances, give the eyes the appearance of being placed half-way up the tentacles, as may be seen in the Potamidae among the Cerithiidae, in *Cypraea*, many Rachiglossa, certain species of *Conus* (Fig. 144, V), and *Pleurotoma*: in the last named they are very near the

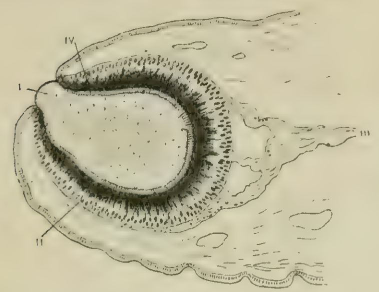


FIG. 100.

Axial section of the eye of *Trochus umbilicaris* I, crystalline lens; II, retina; III, optic nerve; IV, retinidian layer or rods.

extremities of the tentacles in the sub-genera *Drillia* and *Clavatula*. The ocular tubercle is better developed than the tentacle in the Strombidae (Fig. 75 *t*), and finally the tentacle may be aborted and the eye appear to be placed on its summit (*Terebellum*). It is really placed on its summit in *Assiminea* and in the adult terrestrial Pulmonates or Stylommatophora (Figs. 172, 177), but during the development of these forms it is some distance removed from it. In the basommatophorous Pulmonates, and in the Opisthobranchia the eye is at the base of the tentacle, and in the latter group sometimes at some distance from it and often buried beneath the integuments, especially in the Nudibranchia. As regards its structure, the Gastropod eye typically consists of a retina or invagination of the tegumentary epithelium, in which sensory and pigment cells may be distinguished. The former are known as retinophora and are colourless; their free extremities are much contracted, and their opposite extremities are continuous with prolongations of nerve-fibres. The latter, or retinulae, have expanded free extremities, and surround the retinophora. As these two kinds of cells arise by the differentiation of normal epithelial cells, they may not in all cases possess sharply defined characters, and may pass insensibly into one another: the colourless cells actually appear to be absent in the eyes of certain Opisthobranchia that are buried beneath the integuments. The visual organ is completed by accessory structures, of cuticular nature, secreted by the epithelium, and are more distinct from one another in proportion as the eye is more highly specialised. These cuticular structures comprise the layer of rods and the refracting bodies properly so called. The layer of rods, or retinidia, caps the epithelial cells of the retina. These rods, little developed in the Aspidobranchia (Fig. 100, IV), attain their highest degree of specialisation in certain Rachiglossa (Strombidae) and in the Heteropoda (Fig. 101, B, VII). In the last named they are disposed in furrows perpendicular to the optic axis, an arrangement analogous to that found in another pelagic Gastropod, *Gastropteron*. The refractive elements are the crystalline lens—a spheroidal body formed of concentric layers, which does not as a rule fill the cavity of the eye—and a less dense cuticular substance, known as the vitreous body, which surrounds the crystalline lens. In its most primitive condition the visual organ consists simply of an entirely retinal or pigmented invagination, still widely open to the exterior, whose epithelial cells are covered by a layer of rods, but the crystalline lens and vitreous body are altogether absent: this condition is realised in the Docoglossa. In a more advanced stage of specialisation the margins of the invagination become approximated, so that the ocular cavity, whose walls are pigmented throughout their extent, retains a small external aperture, through which water is admitted to bathe the crystalline lens: this condition may be seen in certain Rhipidoglossa, viz. *Pleurotomaria*, the Haliotidae, the Trochidae (Fig. 100), the Stomatellidae, and the Delphinulidae. Finally, the aperture of the ocular cavity is closed, and the crystalline lens is covered in by two superimposed transparent epithelial layers, separated by a transparent layer of connective tissue. These two layers are (1) the internal cornea or "pellucida," a layer of small extent which is simply the anterior continuation of the retina, the two together forming the internal wall of the ocular sphere; and (2) the cornea proper, which is external, and continuous with the tegumentary epithelium. This form of eye is found in all the Rhipidoglossa, with the exceptions mentioned above. In most other Gastropods the structure of the eye is practically the same as in the Rhipidoglossa with a closed cornea, with this difference, that the pellucida is more and the pigmented retina proportionally less extensive. The retinal area becomes more and more restricted in proportion as the eye becomes more specialised—*e.g.* the Heteropoda—or ceases to be functional, *e.g. Guirillea*. There is often a blood space above the pellucida, as may be seen in *Dolium*, the Heteropoda, the Elysiomorpha, and the Basommatophora. As regards the function of the eyes, it has been experimentally demonstrated that aquatic Gastropods are incapable of distinguishing the form of objects, while the terrestrial species are able to distinguish them at a distance of one or two millimetres. The eye becomes rudimentary when it is buried in the integuments; and further, it diminishes in size, though retaining its pigmentation, in the following burrowing Gastropods: several Naticidae (*Natica alderi*, *Amaura*, etc.), various Bullidae (*Scaphander*, *Philine*, *Doridium*, *Gastropteron*, etc.), the Pleurobranchidae, many Nudibranchs, and some Pulmonates, viz. *Siphonaria*, *Auricula midae*, and *A. judae*. The eye may also become rudimentary through loss of its retinal pigment, while still retaining its superficial position: this is the case in species living in situations beyond the reach of the light, whether they be abyssal species (*Guirillea*) or inhabitants of subterranean waters (*Bithynia pellucida*). Finally, regression may be carried so far that the eye, as a consequence of functional disuse, is wholly wanting in the adult state. This phenomenon may be seen in burrowing forms, such as various Naticidae, sundry species of *Terebra*, the Olividae (*Olivella*, *Agaronia*, *Ancillaria*), certain

Marginellidae and *Bullia*; in subterranean Pulmonates, such as *Caecilianella* and *Helix hauffeni*; in abyssal Gastropods, such as *Lepeta*, *Propilidium*, *Bathysciadium*, *Puncturella*, *Cocculina*, a species of *Eulima*, *Choristes*, *Oocorys*, some species of *Fossarus*, *Addisonia*, a species of *Chrysodomus*, *Pleurotoma nivalis*, *Bathydoris*, and *Gonieolis*; in internal parasites, such as the Entoconchidae and *Entosiphon*; among pelagic Gastropoda in *Janthina* and the "Pteropoda."

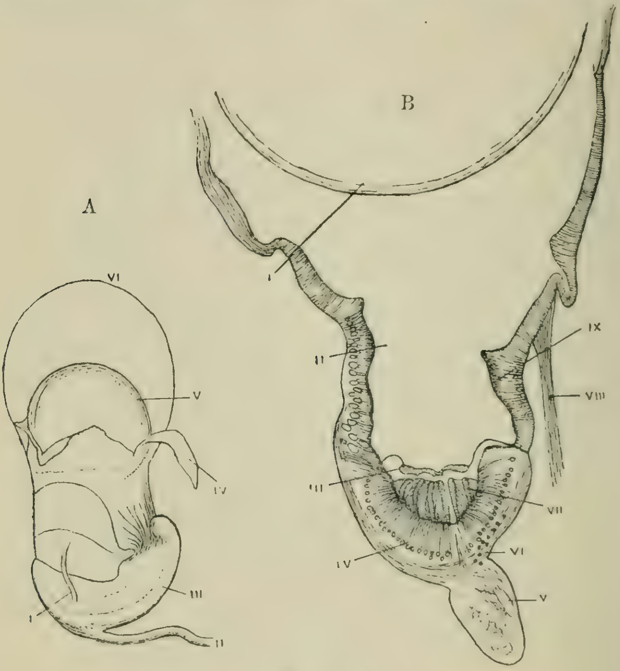


Fig. 101.

Eye of *Pterotrachea*. *A*, the whole left eye. I, retractor muscle; II, optic nerve; III, carina; IV, the pellucida, or inner cornea, lacerated in order to show the lens; V, lens; VI, outline of the pellucida. *B*, sagittal section of the deeper part of the eye. I, lens; II, vitreous body; III, limiting membrane; IV, retina; V, carina; VI, optic nerve; VII, retinal rods on their stands; VIII, retractor muscle; IX, pigmented epithelium. (After Grenacher.)

In addition to the cephalic eyes, certain species of Oncidiidae (*Peronia*) possess a large number of pallial eyes, situated on tubercles on the dorsal surface. Structurally these organs are characterised by the fact that the retinal cells are reversed and their free ends are directed towards the interior of the body, the optic nerve traversing the retina, just as is the case in the vertebrate eye. The optic cavity is filled by a crystalline lens formed of a few large transparent cells. Another example of a pallial eye is found in *Cerithidea obtusa*; in this case it is single, situated in the interior of the respiratory cavity at the anterior extremity of the osphradium, and in it also the optic nerve traverses the retina.

6. *Reproductive Organs.*—The Streptoneura are dioecious, with the exception of the genera *Bathysciadium*, *Cocculina*, *Valvata*, *Marsenina*, *Oncidiopsis*, *Odostomia*, *Entosiphon*, *Entoconcha*, and *Enteroxenos*. All the Euthyneura are monoecious.

In the dioecious Gastropoda sexual dimorphism is generally very slightly marked. The males are externally recognisable only by the penis, when this organ exists; their shape, however, is more elongate than that of the females, and their greatness is often smaller, as, for instance, in Rhipidoglossa, *Paludina*, *Littorina*, various species of *Crepidula*, *Pleurotoma*, etc.: the most typical case in this respect is that of *Lacuna pallidula* (Fig. 7), in which the females are on the average ten times as heavy as the males. In addition, sexual differences are sometimes found in the aperture of the shell (*Littorina obtusata*), in the operculum (some species of *Cerithium*, Quoy and Gaimard), in the radular teeth (certain Buccinidae, Troschel), in the absence of the pedal sucker in the female *Pterotrachea*, of tentacles in the female of some *Firoloida*, and of the slit in the mantle in the male *Vermetus*.

The gonad is always unpaired, even in the most archaic Aspidobranchia. It is generally placed on the dorsal side and at the summit of the visceral mass. It has the form of a racemose gland, made up of a great number of acini, and it may be compact or arborescent, with ramifications extending over and into the liver mass. In Aspidobranchia such as *Pleurotomaria*, the Trochidae, and Fissurellidae the gonad opens into the reno-pericardial duct, in the same manner as in some protobranchiate Lamellibranchs, viz. *Solenomya*. In all other Aspidobranchs, except the Neritacea, the gonad discharges into the kidney. In the Neritacea and Pectinibranchia the reproductive apparatus always possesses its own proper orifice, and there is a genital duct of greater or less length, which, however, is incompletely closed in various Melaniidae, Cerithiidae, Turritellidae, and Vermetidae. This duct opens into the pallial cavity to the right of the intestine in both sexes in the Ampullariidae, and in such forms as have not acquired a penis, that is to say, besides the four families mentioned above, in the Capulidae, Hipponycidae, and Solariidae. In all forms the male duct or spermiduct differs from the female duct or oviduct in the fact that it terminates in a copulatory organ (Fig. 99, XI). In its less specialised form the spermiduct is continued into a seminal furrow or groove (Fig. 85, *r.d'*) which extends from the primitive genital orifice to the extremity of the penis, and is capable of being closed for part of its course, remaining open only in the neighbourhood of or on the penis. This condition is found in a large number of Taenioglossa, viz. *Ampullaria*, the Littorinidae, Modulidae, Struthiolariidae, Chenopodidae, Cassididae, Doliidae, Trotonidae, Naticidae, Cypraeidae, Calyptraeidae, Xenophoridae, Strombidae (Fig. 75, *s.gr*); and in some Stenoglossa, viz. the Muricidae, *Magilus*, *Voluta*, *Lyria*, the Harpidae, *Terebra*, and in all the Heteropoda. In all other forms, that is to say, in a certain number of Taenioglossa and almost all the Stenoglossa, the spermiduct is closed in for the whole of its extent and the penis is hollow (Fig. 44, *h*). Thus the male orifice is secondarily removed to the extremity of the penis, and consequently is at a considerable distance from the primitive position of the genital aperture, a position which is retained by the female aperture. A penis exists in the Neritacea among the Rhipidoglossa, and in all the Pectinibranchia, with the exception of those families of the Taenioglossa enumerated above. When it does not exist copulation cannot take place, and the ova are fertilised in the sea by contact with the spermatozoa emitted by the male. The penis exists only in a rudimentary form in sedentary species, but in all others it is a well-developed, non-invaginable excrescence, situated on the right side of the anterior part of the body, except in cases of *situs inversus*, when it is on the left. All the aerial Streptoneura are necessarily provided with a penis, since in them copulation is indispensable. But the penis is not homologous throughout the group; it is developed at different parts of the body, at the point where the spermiduct ends. Thus the Neritacea have a cephalic penis, as has also *Paludina*, whose penis is a part of the right tentacle. In the Ampullariidae and Cyclostomatidae the penis is developed from the mantle, but in all other forms it is exclusively of pedal origin. Sometimes it is provided with an external whip-like appendage or flagellum: such is the case in many Taenioglossa, viz. nearly all the Littorinidae except *Cremnoconchus*, in *Dolium*, and especially in *Hydrobia*, *Bithynia*, the Naticidae, the Lamellariidae, and the Heteropoda.

The genital ducts are rarely provided with well-differentiated accessory organs in the dioecious Gastropoda. In certain cases there is a glandular tract in the oviduct, which is sometimes specialised to form an albuminiparous gland (*Ampullaria*, *Paludina*, the Naticidae, Lamellariidae and Calyptraeidae, *Triton* and *Cassidaria*). There is a copulatory pouch or receptaculum seminis in the Neritacea, Paludinidae, Cyclostomatidae, and Heteropoda. In some Neritacea—viz. *Neritina*, *Nerita*, *Navicella*, etc.—the receptaculum has its own external opening distinct from the oviducal aperture; this probably corresponds with the right kidney of other Rhipidoglossa, which in this case has been lost by the male sex (Thiele). In some freshwater Taenioglossa, *e.g. Tanganyicia* (Fig. 78) and *Melania episcopalis* (Fig. 109), the oviduct is continued into a ciliated groove which leads to an incubatory pouch situated in the head; this pouch has been homologised with the penis by Moore. The males of *Ampullaria* and the Heteropoda also possess a vesicula seminalis, and the penis frequently is furnished with well-marked superficial glands (Littorinidae, *Cassis*, *Terebra*, and the Heteropoda). In some Taenioglossa, such as *Paludina* and *Pteroceras*, and in several Stenoglossa, such as *Murex*, *Nassa*, *Purpura*, etc., there are two kinds of spermatozoa, the one normal and filiform, the other vermiform; the function of the latter kind is not yet explained. In *Paludina*, for example, these two kinds of spermatozoa exist in equal quantities, but the filiform kind, with a single cilium, originate from spermatids which have increased but little in size during the growth period, and contain the normal quantity of nuclear substance: these are the eupyrenic spermatozoa of Meves. The vermiform spermatozoa, on the other hand, have about six cilia apiece, originate from spermatids which have increased largely in size during the growth period, and contain only a small quantity of nuclear substance: they are known as oligopyrenic spermatozoa.

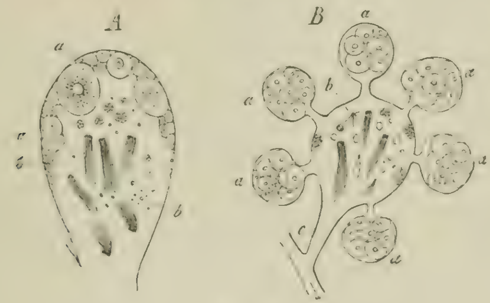


FIG. 102.

Follicles of the hermaphrodite gonads of Euthyneura. *A*, of *Helix*; *B*, of *Eolis*. *a*, ova; *b*, developing spermatozoa; *c*, common efferent duct. (From Lankester, after Gegenbaur.)

In the monoecious Gastropods the gonad ordinarily occupies the same position and has the same relations as in the dioecious Streptoneura, but it may be much more subdivided, especially in certain Nudibranchs, viz. *Phyllirhoë* (Fig. 161, *g*) and Elysiomorpha. It has always a duct with its proper external orifice and a penis which is invaginable in most Euthyneura, but this latter organ is absent in hermaphrodite parasitic Streptoneura. The gonad differs from that of the dioecious Streptoneura in producing ova and spermatozoa in the same individual. In the most simple arrangement the two kinds of genital products are developed side by side, as may be seen in *Valvata* and in the majority of the Tectibranchia and Pulmonata (Fig. 102, A). In the more specialised condition there are male and female acini, the latter opening into the spermatogenous sacs in *Oncidiopsis*, the Pleurobranchidae, the majority of the Nudibranchia (Fig. 102, B), with the exception of the Elysiomorpha. *Entoconcha*, *Enteroxenos*, and *Bathysciadium* are the only genera in which the male and female acini are quite distinct. In its most primitive condition the genital duct is hermaphrodite, that is to say, it is a spermoviduct throughout its length, and is therefore called monaulic. It generally is provided with an internal double longitudinal fold. The hermaphrodite aperture is situated on the right side, near the opening of the pallial cavity, and is connected by a ciliated seminal groove with the more anteriorly situated penis. This condition is found in the Bullomorpha (Fig. 98, *s.g*) in general, including the Thecosomata ; in the Aplysiomorpha (Fig. 154, *i*), including the Gynmosomata (Fig. 84, IV, XI); and in the Pulmonata *Pythia* (Fig. 171). The edges of this seminal groove unite to form a complete tube in *Carolinia longirostris* among the Bullomorpha, and among the Pulmonata in all the Auriculidae except *Pythia*, and as a consequence the primitive genital aperture serves only for the emission of the female products, the male products passing through a spermiduct closed throughout its extent. In subsequent stages of evolution of the genital duct the spermiduct takes its origin from the hermaphrodite duct above the external opening: this latter duct, therefore, bifurcates or becomes "diaulic," the female branch of the duct opening by the primitive hermaphrodite orifice. This condition is characteristic of *Valvata* and *Oncidiopsis* (Fig. 103), of *Actaeon* and *Lobiger* among the Bullomorpha, of the Pleurobranchidae and the Nudibranchia except the Doridomorpha and most of the Elysiomorpha, and of the Pulmonata. At the point of bifurcation the male and female sections of the duct are separated by a narrow slit, which only allows the spermatozoa to pass. In this case therefore, as in the dioecious Gastropoda, the female orifice remains in the same place as the primitive genital aperture, and the male orifice is carried far forward, to the extremity of the penis. The two external orifices, male and female, are thus at some distance from one another, as may be seen in *Valvata*, *Oncidiopsis* (Fig. 103, *f.o*, *pe*), the Basommatophora in general, the Oncidiidae (Fig. 59, *o.f*, *o.m*), and *Vaginula* (Fig. 87, *o.f*). But the female aperture itself may be secondarily shifted from its original position, and come so near to the penial aperture as to be contiguous to it, a condition found in the Pleurobranchidae and the Nudibranchs in general ; or the two apertures may reunite in a common cloaca, as in the Stylommatophora (Fig. 177, II), *Siphonaria*, and *Amphibola*. In these various cases the female duct, like the hermaphrodite duct of the monaulic forms, bears a bursa copulatrix or receptaculum seminis, which in certain stylommatophorous Pulmonates, such as *Helix aspersa*, *Clausilia*, etc., is provided with an accessory branch (Fig. 104, *R.s*).

A third differentiation of the genital ducts is brought about when the female duct becomes bifurcated through the separation of the bursa copulatrix, the latter acquiring a separate external aperture but remaining in connection with the oviduct by its deeper extremity. In this manner two female orifices are formed; the one is the copulatory orifice, the other is the oviducal orifice serving for the passage of the ova. The genital duct is thus trifurcated or "triaulic," a condition which is not found in any Pulmonate, but is confined to certain Nudibranchs, viz. the Doridomorpha and the majority of the Elysiomorpha (Fig. 105).

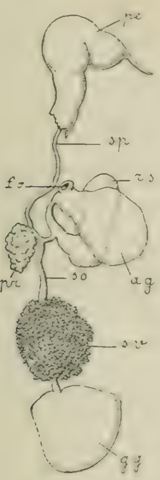


Fig. 103.

Oncidiopsis, hermaphrodite genital apparatus, dorsal view. *a.g*, albuminiparous gland; *f.o*, female orifice; *g.g*, hermaphrodite gonad; *pe*, penis; *pr*, prostate; *r.s*, receptaculum seminis; *so*, spermoviduct; *sp*, spermiduct; *s.v*, seminal vesicle.

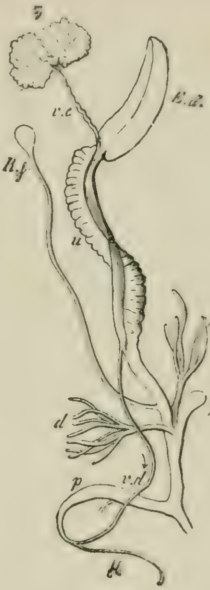


Fig. 104.

Hermaphrodite reproductive apparatus of *Helix hortensis*. *d*, digitate accessory glands on the female duct; *E.d*, albuminiparous gland; *fl*, flagellum; *p*, penis; *p.s*, calciferous gland or dart-sac on the female duct; *R.s*, receptaculum seminis or spermatheca, opening into the female duct; *u*, uterine dilatation of the hermaphroditic duct; *v.d*, spermiduct or vas deferens; *v.e*, hermaphroditic duct; *z*, ovo-testis. (From Ray Lankester, after Gegenbaur.)

The penis is invaginable in all the Euthyneura with the exception of *Actaeon* (Fig. 148, VI) and *Umbrella*. It is a pedal structure in nearly all Opisthobranchia, but in *Umbrella* it is cephalic. In the majority of Pulmonates the penial nerve arises from the cerebral ganglion, but the fibres of the nerve originate from the pedal and only traverse the cerebral ganglion. In monaulic species the penis often bears an appendage, and occasionally chitinous accessory structures: there is a single stylet in several species of *Planorbis*, in *Glaucus*, and many other

Nudibranchs, the stylet being contained in a special pouch in certain species of *Doris*: in some other Nudibranchs there are multiple stylets.

In addition to the bursa copulatrix, there are numerous and various accessory genital organs in the hermaphrodite Gastropoda. An albuminiparous and a mucous gland are found on monaulic ducts, generally near their distal end (Fig. 171, *muc*). In the diaulic Pulmonata there is a large albuminiparous gland on the hermaphrodite section of the duct (Fig. 104, *E.d*), and on the female part of the duct of Basommatophora there is an albumen gland corresponding to the uterine glands of Stylommatophora (Fig. 104, *u*). The diaulic and triaulic Opisthobranchs have also contiguous albumen and mucous glands on the oviducal part of the genital duct. The terminal portion of the oviduct of Stylommatophora is further provided with a glandular zone (*Zonites*), or with two multifid vesicles with a variable number of ramifications (Fig. 104, *d*). Opening between the two is a special pouch—seemingly a specialised multifid vesicle, which secretes a sharp calcareous dart (Fig. 104, *p.s*). Before copulation the dart-sac is evaginated together with all the terminal part (vestibule) common to the reproductive organs, and the dart, which is caducous, pierces the skin of the conjugate. The spermiduct is sometimes furnished with a more or less elongate "prostate" gland, as in *Valvata*, *Oncidiopsis* (Fig. 103, *pr*), various Bullomorpha and Elysiomorpha (Fig. 105, *pr*). The penis of certain Stylommatophora is provided with a long hollow caecum, the "flagellum" (Fig. 104, *fl*), in the interior of which is secreted the spermatophore or capreolus. This is a thin-walled chitinous tube closed at one end and cleft at the other and filled with a quantity of sperm. When there is no flagellum the spermatophore is formed by the deeper portion of the penis. Sometimes the spermatophores are furnished with denticulations and even with arborisations (Fig. 106).

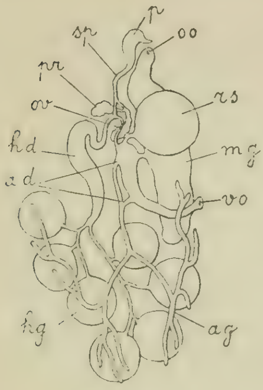


Fig. 105.

Limapontia, reproductive apparatus, dorsal aspect. *a.d*, albuminiparous duct; *a.g*, albuminiparous gland; *h.d*, hermaphroditic duct; *h.g*, ovo-testis; *m.g*, mucous oviducal gland; *o.o*, oviducal orifice; *ov*, oviduct; *p*, penis; *pr*, prostate; *r.s*, receptaculum seminis: *sp*, spermiduct; *vo*, vulva.

The hermaphrodite gland (gonad) does not liberate ova and spermatozoa simultaneously, the discharge of the former occupying a very short time after copulation. Generally speaking, the hermaphroditism is protandric, the spermatozoa being the first of the genital products to come to maturity. This hermaphroditism is not self-sufficient, and the union of two individuals is necessary for fertilisation. There are, however, instances of Pulmonates which have been insolated from the time of birth and have nevertheless laid eggs which have developed (*Zonites cellarius*, *Limnaea*). In all species possessing a penis, fertilisation is effected by copulation; in species without a penis—*e.g.* *Patella*—artificial fertilisation is possible. During the venereal act the penis is thrust into the bursa copulatrix, when this latter structure is present, and discharges into it a quantity of sperm which subsequently fertilises the ova during their passage down the oviduct. Copulation and the act of oviposition that follows it take place at various seasons. In temperate regions they continue from early spring onwards, extending even into the winter, as is the case in *Patella* in the Atlantic and *Trochus striatus* in the Mediterranean. In the stylommatophorous Pulmonates with a common genital orifice, the two copulating individuals mutually fertilise one another, each one acting as male and female, and the same is the case in the majority of Nudibranchs. In the hermaphrodites with distant genital apertures the same animal may act as male and female, but as a rule not simultaneously, unless, indeed, it unites with two or more individuals to form a chain, as may be seen in *Limnaea*, the Aplysiomorpha, etc. The copulation of two individuals is effected in the same manner as in the dioecious Gastropoda (Fig. 107).

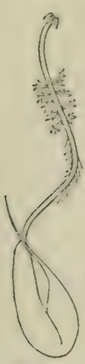


FIG. 106.

Spermatophore of *Nanina wallacei*, magnified. (After Pfeffer.)

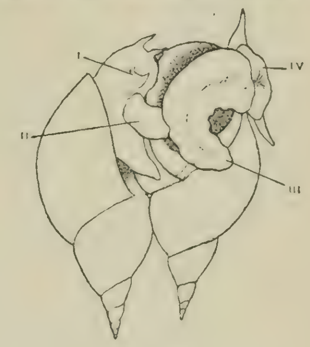


FIG. 107.

Two *Limnaea stagnalis* in copulation, the left one acting as male. I, tentacle and eye; II, penis; III, foot; IV, buccal veil. (After Stiebel.)

III. EMBRYOLOGY.

The eggs may be laid or may develop within the maternal organism. In the oviparous species that do not copulate, the unfertilised ova are generally laid one by one and are not united by an accessory envelope (Patellidae, *Haliotis*, certain Trochidae of the sub-genera *Gibbula* and *Trochocochlea*), but in Fissurella and in Trochidae of the sub-genus *Zizyphinus* they are united by a gelatinous investment. In the species that copulate the ova are deposited within a few days after the act of copulation, the time varying from one day in sundry Nudibranchs to as many as fifteen days in some species of *Helix*. The nidus may assume very various shapes. In aquatic species the shells surrounding the eggs may be embedded and united in a single gelatinous mass, which may be ribbon-shaped, more or less coriaceous, attached in littoral species, floating in pelagic species. This is more especially the case in the Euthyneura—viz. in the Basommatophora and Opisthobranchia, in which the ribbon is often coiled into a spiral—and also in many Taenioglossa (Littorinidae, Rissoidae, Hydrobiidae, etc.). In such cases each egg-shell contains a single ovum. Again, the egg-shells may be coriaceous (Rachiglossa), more or less independent, simply attached to one another (*Buccinum*, *Fusus*, *Pyrula*), or fixed side by side on a common support (*Purpura*, *Murex*, *Nassa*, Fig. 108, *Trophon*, *Voluta*, etc.). In this case each shell contains a considerable number of ova, but all of them do not complete their development. As special forms of nidus may be mentioned that of *Natica*, in which the eggs are united by agglutinated sand into a horny-looking ribbon coiled in a ring; that of *Lamellaria*, whose eggs are deposited in a sort of nest excavated in colonies of Synascidians. Finally, various forms of Streptoneura attach their eggs to various parts of their bodies, and thus appear to be more or less incubatory, as, for instance, Hipponycidae and Capulidae (in *Calyptraea* the eggs are attached below the neck); or they may attach them to the external surface of the shell, *e.g.* *Neritina*, *Hydrobia ulvae*, and in exceptional cases *Rissoa*; or to the internal face of the shell, *e.g.* *Vermetus* (Fig. 45, *ov*). In the oviparous *Janthinae* the eggs are attached to the float (Fig. 135, *b*).

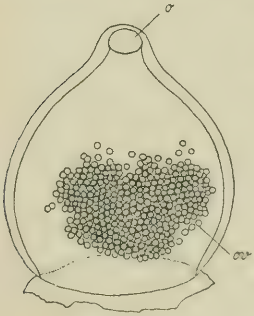


FIG. 108.
Egg-capsule of *Nassa reticulata*, × 12. *o*, aperture; *ov*, eggs.

The stylommatophorous or terrestrial Pulmonates generally lay in the earth isolated ova enclosed either in a gelatinous envelope (*Limax*, etc.) or in a calcified shell, *e.g.* certain species of *Helix*, *Testacella*, etc. In *Bulimus* these eggs may attain a length of three centimetres, thus exceeding in size the eggs of many birds. The eggs of *Ampullaria* have also a calcified envelope; they are laid in the water and are agglomerated together. When *Succinea* lays its eggs in the water it surrounds them with a gelatinous mass, like the basommatophorous Pulmonates.

In the ovoviviparous Gastropoda the progeny are born living after undergoing their development within the parent. They develop in the terminal portion of the oviduct in the following Streptoneura: *Paludina*, *Typhobia*; various species of *Melania* (Fig. 109), *Littorina*, *Cymba*, *Janthina*, *Nassopsis*, and the Entoconchidae; in the Opisthobranch *Halopsyche*; and in numerous Pulmonates—viz. *Glandina algira*, *Rhytida aequalis*, *Selenites voyanus*, *Helix rupestris*, *H. inversicolor*, *H. inaequalis*, *H. unidentata*, *H. erronea*, *H. studeriana*, *Patula cooperi*, *Acanthinula harpa*, the genera *Partula*, *Balea*, *Coeliaxis*, *Pupa muscorum*, *P. umbilicata*, *P. cylindracea*, *Clausilia ventricosa*, *C. similis*, *Achatina alabaster*, and *A. zebra*, *Stenogyra mammillata* (Fig. 8), *S. octona*, *S. terebraster*, *S. dominiciensis*, *S. decollata*, *S. lamellata*, *Ferussacia folliculus*, *F. lamellifera*, *F. procerula*, *F. debilis*, *Vaginula vivipara*. The embryos develop in a special incubatory pouch excavated in the interior of the foot and connected with the extremity of the ciliated canal which passes from the female orifice to the head in *Melania episcopalis* (Fig. 109, *b.p.*) and *Tanganyicia rufofilosa* (Fig. 78, *b.p*).

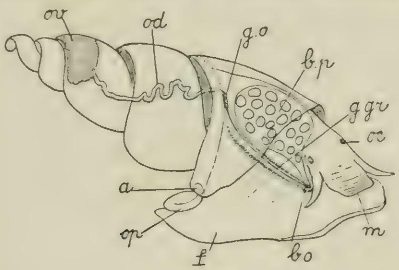


FIG. 109.

Melania episcopalis, out of its shell, showing the female genital apparatus, right-side view. *a*, anus; *b.o*, brood-pouch opening; *b.p*, brood-pouch; *f*, foot; *g.gr*, genital ciliated groove; *g.o*, genital orifice; *m*, mouth; *oc*, eye; *od*, oviduct; *op*, operculum; *ov*, ovary. (After Moore.)

In viviparous Gastropods the ovum contains but little yolk, but in other forms the quantity of deutoplasm is greater, and is especially large in a number of Rachiglossa, such as *Nassa*, etc. The segmentation of the ovum is always total, and, except in cases in which the deutoplasm is scanty (*Paludina*), it soon becomes irregular. As a rule in Aspidobranchia, Taenioglossa, and Pulmonata, the two first cleavage planes are meridional, the first separating the right and left halves of the future animal. The third cleavage is equatorial and cuts off the micromeres at the animal pole from the macromeres at the opposite pole, so that, as a rule, there are four macromeres from the beginning (Fig. 9, A, B). These macromeres give rise to two more generations of micro- or ecto-meres, and the latter proliferate very rapidly. In such forms as *Patella*, *Planorbis*, and *Limax*, the blastula formed in this manner contains a large blastocoel between the micromeres and macromeres, but in other Gastropods this cavity is much reduced. In some

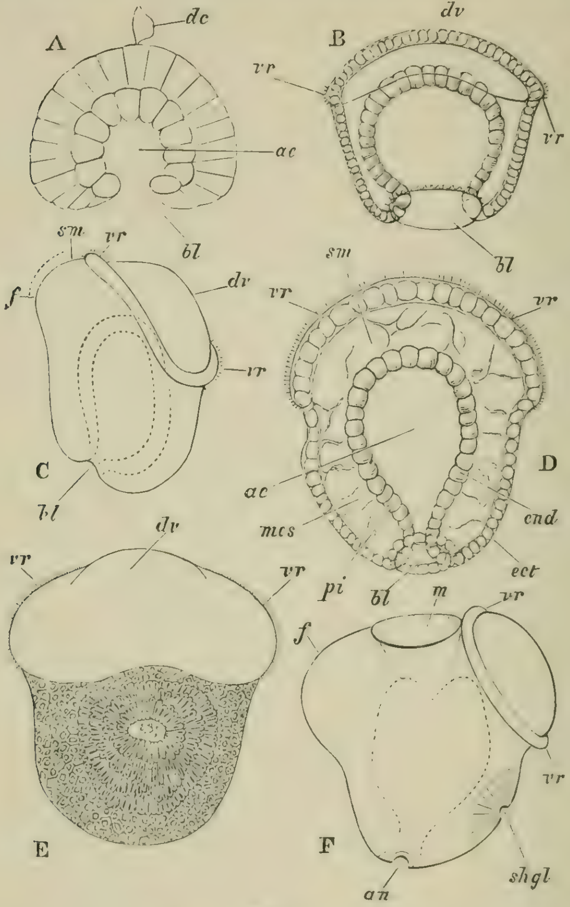


FIG. 110.

Development of the river-snail (*Paludina vivipara*), in which the mouth and stomodaeum are formed independently of the blastopore, the latter persisting as the anus. *ac*, archenteron, or endodermic cavity; *an*, anus; *bl*, blastopore; *d.c*, directive or polar corpuscle; *d.v*, velar area or cephalic dome; *f*, foot; *m*, mouth; *mes*, rudiments of the mesoderm; *p.i*, pedicle of invagination, the future rectum; *sh.gl*, the shell-gland; *s.m*, site of the as yet unformed mouth; *vr*, velum. *A*, Gastrula phase (optical section). *B*, the Gastrula has become a Trochosphere by the development of the ciliated velar ring (optical section). *C*, side view of the Trochosphere with commencing formation of the foot. *D*, further advanced Trochosphere (optical section). *E*, the Trochosphere passing into the Veliger stage; dorsal view showing the formation of the shell-gland. *F*, side view of the same, showing foot, shell-gland, velum, mouth, and anus. (After Lankester.)

types such as *Paludina*, *Planorbis*, etc., the endoderm formed by the macromeres is invaginated into the ectodermic layer formed by the micromeres, but in many cases, in consequence of the far more rapid multiplication of the micromeres and the much larger size of the macromeres, gastrulation is effected by epiboly, and the endoderm is invaginated at a later period; in this case the endodermic cavity or enteron is of small size. In most cases the blastopore closes, and the definitive mouth is formed by a new invagination at the point of closure: it is only in *Paludina* that a portion of the blastopore remains open and becomes the anus (Fig. 110, C, *bl*; F, *an*). The mesoderm is formed as two primary mesomeres from the more posterior of the two primitive macromeres (Fig. 11, *mes*). The mesodermic organs (definitive kidney, heart, etc.) do not arise until a late period, their place being taken, during the development, by provisional larval organs, such as superficial contractile sinuses and larval kidneys (Figs. 114, 118).

The ciliated trochosphere larva is sometimes constituted at a very early period, before the formation of the mesoderm — *e.g.* in *Patella*, *Acmaea*, and *Trochus*—and in such cases the embryo becomes free at once. But in most cases the larva is not hatched out until a much later period, and a large part of the development is effected within the egg envelope. The larva—whose shell is often different from that of the adult—is characterised by its velum and by some other external or superficial larval organs.

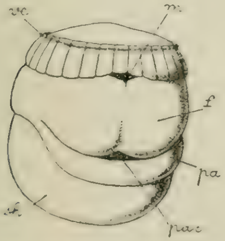


Fig. 111.

Young veliger of *Trochus*, ventral aspect. *f*, foot; *m*, mouth; *pa*, mantle; *pa.c*, pallial cavity; *sh*, shell; *ve*, velum. (After Robert.)

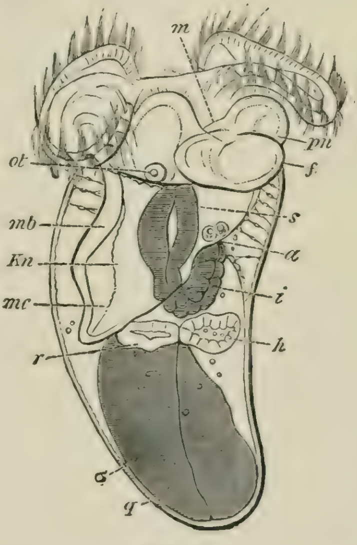


Fig. 112.

Larva of *Cavolinia tridentata*, ventral aspect. *a*, anus; *f*, median portion of the foot; *h*, heart; *i*, intestine; *Kn*, contractile sinus; *m*, mouth; *mb*, mantle-skirt; *mc*, subpallial chamber; *ot*, otocyst; *pn*, lateral lobe of the foot (the future left fin); *q*, shell; *r*, kidney; *s*, oesophagus; σ, sac containing nutritive yolk. (From Lankester, after Fol.)

The *velum* is the locomotory ciliated ring, which arises antero-dorsally (Fig. 110, C, *vv*) and circumscribes the apical area. As in the Amphineura, it is only slightly prominent in the most archaic marine Aspidobranchia (*Patella*, Fig. 14, *Acmaea*, *Trochus*, Fig. 111, *ve*), but in other Gastropods it becomes more and more prominent, and eventually gives rise to a natatory velum formed of two lateral lobes with ciliated margins (Fig. 112). These lobes may in turn be subdivided into two (Fig. 121, *ve*) or three secondary lobes (for example, in *Atlanta* and in "*Ethella*," a larval form attributed to one of the Strombidae). In viviparous species, or in forms like *Cenia* and the Pulmonata, in which the young are hatched in the adult condition, the velum becomes rudimentary or disappears altogether; in the Basommatophora (Fig. 119, A) it is developed to a slight degree, but only on the sides, and is not continuous; in the Auriculidae, Siphonariidae, and Oncidiidae, however, all of which are marine, a normal velum is present.

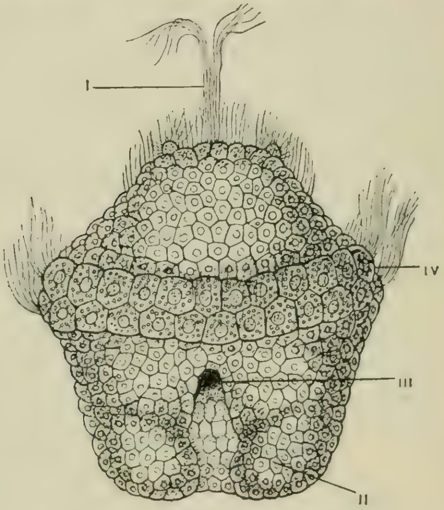


FIG. 113.

Trochosphere of *Patella*, in the 34th hour. I, flagellum in the apical area; II, left lip of the blastopore; III, blastopore; IV, velum. (After Patten.)

The *foot* is always very short at first (Fig. 1, *f*), being represented by a mere papilla, which in sundry instances is formed from two paired rudiments (Fig. 113, II) situated between the two extremities of the primitive blastopore when this latter structure is elongated. The operculum is formed early, and exists in all testaceous larvae, even in cases in which the adult possesses neither shell nor foot: the only exceptions to this statement are the Pulmonata (excepting the Auriculidae, the Amphibolidae, and the

Siphonariidae), the Cavoliniidae, and the Gymnosomata. The pedal glands are formed by ectodermic invaginations, and in some species exist in the larva though they are absent in the adult (*Purpura*).

The preconchylian invagination or shell-gland (Fig. 110, *sh.gl*) appears at the beginning of development in the centro-dorsal area behind the velum, on the side of the body opposite to the blastopore. It is surrounded by a ridge which gradually extends over the visceral sac and secretes the shell (Fig. 117, *sh*). In some Stylommatophora —viz. *Clausilia* and *Succinea*, a pallial sac is formed which covers up the shell, but eventually opens again. The shell grows in thickness internally, fresh matter being added to it from the external surface of the mantle, but its increase in extent is dependent on the activity of the border of the mantle, where there are special glands which degenerate when the animal reaches the adult state. It is only at this period that the aperture of the shell acquires a lip, or is contracted in various ways to form, for example, the linear aperture of *Cypraea*, *Cavolinia*, etc. In Gastropoda that are naked in the adult state, the shell falls off soon after the reduction of the velum (Fig. 116), but in *Cenia*, *Runcina*, and *Vaginula* the shell-gland and shell are not developed, and the young animal, at the time of escaping from the egg, has already the naked form of the adult.

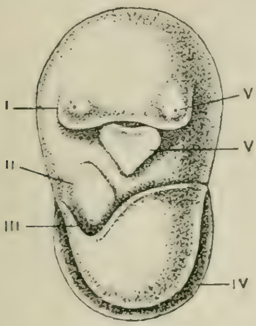


Fig. 114.

Embryo of *Vermetus*, ventral aspect. I, velum; II, contractile sinus ("embryonic heart"); III, opening of the pallial cavity; IV, shell; V, foot; VI, left eye. (After Salensky.)

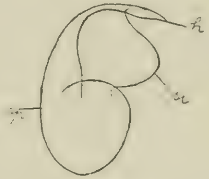
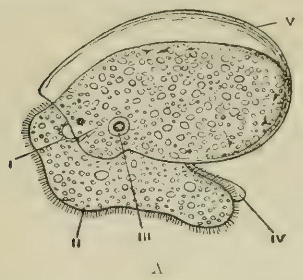


Fig. 115.

Larval shell of *Nassa reticulata*, ventral aspect, × 30. *h*, hook of the dorsal edge of the aperture; *si*, future canal or shell-siphon; *sp*, spire.

The superficial contractile sinuses are portions of the wall of the body, temporarily modified to ensure the circulation of the nutritive fluid in the system of cavities destined to become the circulatory apparatus of the adult. In the walls of these sinuses are muscular elements, whose fibres are sometimes disposed in regular meshes, as, for example, in the nuchal sinuses of the Rachiglossa. These organs are acquired in the course of ontogeny, and are developed in different regions: they are frequently found between the foot and anus, in front of the pallial cavity, *e.g.* *Helix*, *Bithynia*, *Vermetus*, the Rachiglossa, and nearly all the marine Gastropoda, including the "Pteropoda," Heteropoda, and Nudibranchia. This sinus is displaced, together with the pallial aperture, along the right side towards the neck (Fig. 114, II), and finally is partly contained in the pallial cavity. In the Basommatophora there is a velar dorsal sinus, and in the Stylommatophora, *Arion*, *Limax*, *Clausilia*, *Helix*, etc., but not in *Succinea*, there is a caudal vesicle, known as the pedal sinus or podocyst (Fig. 117, *po*).



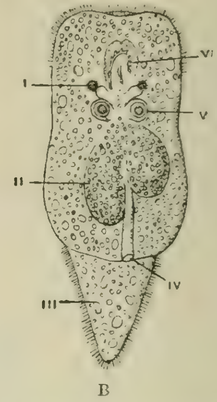


FIG. 116.

Larvae of *Eolis* (*Galvina*) *exigua*. *A*, on the second day, left-side view. I, radula; II, foot; III, otocyst; IV, operculum; V, shell. *B*, on the third day, after the loss of the shell, dorsal aspect. I, eye; II, left liver lobe; III, foot; IV, anus; V, octocyst; VI, radula. (After Schultze.)

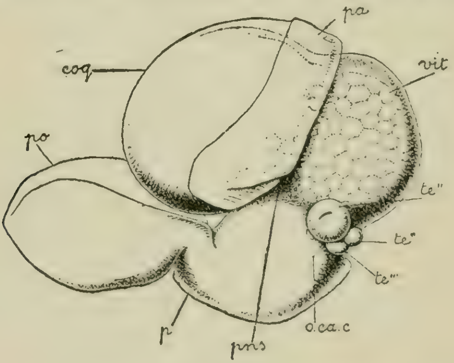


FIG. 117.

Helix aspersa, embryo of the tenth day, right-side view. *coq*, shell; *o.ca.c*, external opening of the cerebral cavity; *p*, foot; *pa*, mantle; *po*, contractile vesicle or podocyst; *te''*, the true tentacles; *te'''*, labial palp; *vit*, vitellus.

The larval kidneys are paired and generally symmetrical organs situated at the anterior end of the body, immediately behind the velum or apical area. In the marine Streptoneura they are caducous ectodermic projections, in which the products of excretion are accumulated. In the Opisthobranchs they are closed pouches; in *Paludina*, *Bithynia*, and the Pulmonates they are canals opening to the exterior. In the last-named group these organs consist of tubes of ectodermic origin, each of which bears an ampulla on the middle of its course, and its internal portion is formed of perforated cells and ends internally in a closed flame-cell. In the Basommatophora (Fig. 118, *re*) these cells of the larval kidney are four in number, three being perforated and one a flame-cell. These organs are absent in *Vaginula*.

The nerve-centres and organs of special sense originate from the ectoderm, almost always from an ectodermic thickening on the buccal side of the apical organ of the larva (*Crepidula*), but in *Vermetus* and the Cavoliniidae an ectodermic invagination has been described as taking part in the formation of each cerebral centre. Again, in the Pulmonates, even if the principal part of the cerebral centres is formed from an epithelial thickening, the posterior accessory lobe originates from a subsequent ectodermic invagination (Fig. 117, *o.ca.c*)—the "cerebral tube"—the cavity of which generally disappears after the animal is hatched out, but persists in the adult *Planorbis* and *Limnaea*. The eyes arise in the velar field, near the cerebral centres, and are formed by invagination in the Aspidobranchia, *Paludina*, the Stylommatophora, etc., but from thickenings in *Vermetus*, and frequently after the veliger larva is hatched, as, for example, in many Nudibranchia, with the exception of the Tergipedinae (Fig. 61, *e*). The otocysts are always formed at an early stage, on the antero-lateral aspects of the foot, by invagination in the majority of marine Gastropods, but from ectodermic thickenings in many Pulmonata. At first they invariably contain a single otolith, even in the species which in the adult state possess multiple otoconia. In pelagic larvae the otocysts may often be seen to be asymmetrical, and sometimes the tentacles share this peculiarity

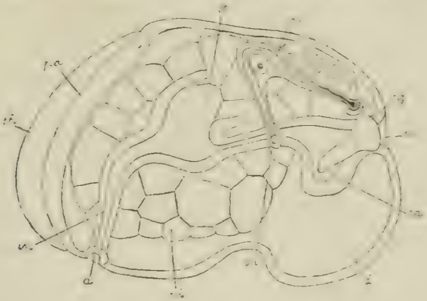


FIG. 118.

Embryo of *Limnaea stagnalis*, viewed from the right side. *a*, anus; *c.g*, cerebral ganglion; *f*, foot; *in*, intestine; *m*, mouth; *o.r*, aperture of the embryonic kidney; *pa*, mantle; *ra*, radula; *re*, embryonic kidney; *sh*, shell; *st*, stomach; *vi*, vitellus. (After Erlanger.)

As regards the formation of the internal organs of the adult, the stomach, the liver, and nearly the whole of the intestine arise from the endoderm. The liver lobes are formed before the absorption of the nutritive sacs borne on the posterior part of the larval stomach. The proctodaeal invagination, placing the intestine in communication with the exterior, is always of small importance, but, on the other hand, the buccal bulb and oesophagus, with their numerous accessory organs, are formed from an important stomodaeal ectodermic invagination, which always corresponds in position with the extreme anterior end of the blastopore, whether the latter is closed or remains open. The remaining organs are formed in the same manner as in other Mollusca, as has been described in the first chapter, and the ontogeny of the Gastropoda does not exhibit any special features other than certain post-larval metamorphoses and the torsion produced during development (Fig. 51).

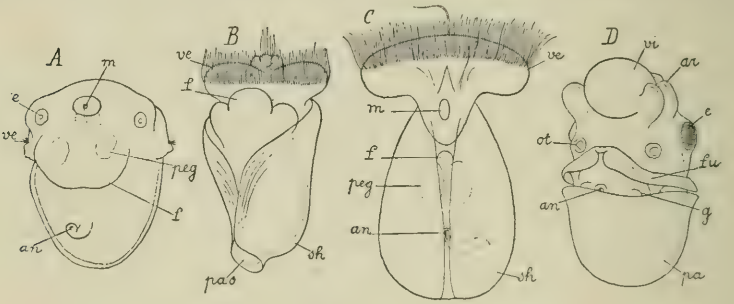


FIG. 119.

Embryos and larvae of various Molluscs, after the ventral flexure and before the torsion (for *A*), ventral aspect. *A*, Gastropod (*Limnaea*, after Fol); *B*, *Dentalium* (after Lacaze); *C*, Lamellibranch (*Dreissensia*, after Meisenheimer); *D*, Cephalopod (Oigopsid, after Grenacher). *an*, anus; *ar*, arms; *e*, eye; *f*, foot; *fu*, funnel; *g*, gill; *m*, mouth; *ot*, otocyst; *pa*, mantle; *pa.o*, posterior pallial orifice; *pe.g*, pedal ganglion; *sh*, shell; *ve*, velum; *vi*, vitellus.

Up to the trochosphere stage the larva is strictly symmetrical (Fig. 14, B), but afterwards the torsion sets in, as a result of which the asymmetry characteristic of adult Gastropoda is established. At first the aperture of the pallial cavity and the anus are always posterior (Fig. 118), as is the case in all symmetrical Molluscs (Fig. 22, A, B, D, E); then they are carried forward by a *ventral flexure* (Fig. 119) in the same manner as in the Cephalopoda, Scaphopoda, and many Lamellibranchia. But in the Gastropods a lateral torsion is superadded to this primitive flexure, causing the pallial aperture to pass from the postero-ventral surface (Fig. 51, A) over to the right side (Fig. 51, B), and thence to the antero-dorsal surface (Fig. 51, C). If the animal be supposed to have the mouth turned towards the observer, this torsion may be seen to follow the movements of the hands of a watch (Fig. 52).

Post-larval metamorphoses occur in various cases. The velum, as seen above, disappears, being absorbed by a process of phagocytosis. In various genera the operculum falls off, and so also does the shell in naked forms (Fig. 116, B) and in *Lamellaria*, in which a new shell is formed replacing the larval shell or *Echinospira*.

It is only in rare cases that a second larval form exists after the disappearance of the velum and before the adult state is reached; this is the case, however, in the gymnosomatous "Pteropods," in which three transverse and parallel ciliated rings are formed before the fins are completely developed (Fig. 120). The most anterior of these rings is made up of interrupted portions; the two others, on the contrary, are continuous, and are situated respectively at the middle of the body and near the aboral extremity. These two continuous ciliated circles, and especially the more posterior, are preserved till a very late period, and sometimes persist in the adult, whose habits do not differ from those of the larva (Fig. 155).

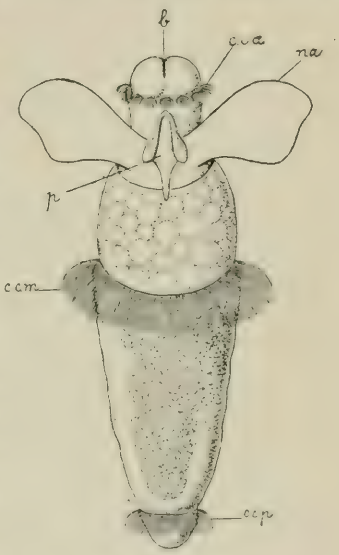


FIG. 120.

Larva of *Spongiobranchaea australis*, ventral aspect. *b*, mouth; *c.c.a*, anterior ciliated ring; *c.c.m*, middle ciliated ring; *c.c.p*, posterior ciliated ring; *na*, fin; *p*, foot. (After Racovitza.)

Sooner or later after their expulsion from the oviduct, or after the nidus is laid, the eggs are hatched out: after a period of some twenty hours in *Trochus*, after ten days in certain Nudibranchs (*Tergipes*), at the end of eighteen days in others (*Cenia*), after three or four weeks in *Limnaea*, after more than a month in *Valvata* and certain species of *Arion* and *Limax*. It is only in exceptional cases that the young are hatched out with the characters of the adult, but this is the case in all the Pulmonates — with the exception of the Siphonariidae which have a marine veliger larva—in the Opisthobranchs *Cenia* and *Runcina*, and in sundry Streptoneura such as *Littorina* and *Lacuna* among the Taenioglossa, and *Purpura* and *Buccinum* among the Rachiglossa. In normal cases the young Gastropods are hatched out as free-swimming or pelagic veliger larvae (Fig. 61). This veliger has a very small foot and a more or less voluminous velum, the latter organ being smallest in the least specialised forms, such as *Trochus* (Fig. 111), *Patella*, *Fissurella*, etc., and is the characteristic larval form in most opisthobranchiate

Euthyneura and in the majority of Streptoneura. Even in those Gastropods that are hatched out in the adult form, the veliger stage can generally be recognised, in a more or less reduced condition, within the egg membranes, *e.g.* in *Buccinum*, *Cenia*, the basommatophorous Pulmonates. In all Gastropods the velum is reduced in proportion as the foot develops; nevertheless, in a considerable number of pelagic larvae the veliger stage is preserved for a long time, and the velum persists, and often develops excessively long lobes even after the creeping foot is fully and normally developed: such is the case in "*Macgillivraya*" (Fig. 121), "*Agadina*," "*Cheletropis*," "*Sinusigera*," "*Echinospira*," etc., all of which are special pelagic larval forms of Streptoneura which were long considered to be distinct genera. The velar lobes may even produce lobate expansions of the margin of the aperture of the shell, but these disappear when the velum is absorbed and the shell assumes the adult form (Fig. 122).

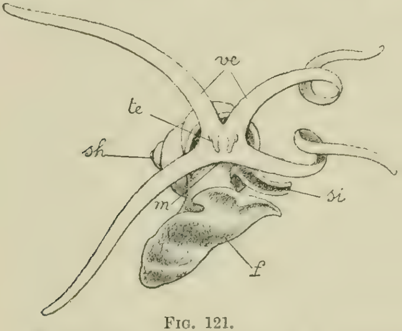


FIG. 121.

"*Macgillivraya*," pelagic larva of a siphonate Streptoneurous Gastropod (*Dolium*), ventral aspect, × 12. *f*, foot; *m*, mouth; *sh*, shell; *si*, siphon; *te*, tentacle and eye; *ve*, lobes of the velum. (After MacDonald.)

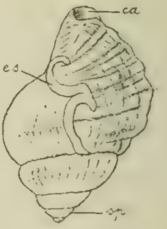


FIG. 122.

Shell of a young *Purpura haemastoma*, enlarged, dorsal aspect. *ca*, canal of the adult; *e.s*, limit of the embryonic shell; *sp*, spire. (After Dautzenberg.)

IV. DEFINITION.

The asymmetry of some of the principal organs of the body is the chief characteristic of the Gastropoda. The essential feature of this asymmetry is that the anus generally lies to one side of the median plane; that the ctenidium, the osphradium, the hypobranchial gland, and the auricle of the heart are azygos, or at least are more developed on one side of the body than the other; and that there is only one genital orifice, which lies on the same side of the body as the anus. In other words, one-half—generally the morphologically left but topographically right half—of the anal complex is either atrophied or has disappeared altogether. This asymmetry, expressed by the transfer of the morphologically right organs to the left side, is the result of a torsional movement, which has carried the anus and pallial cavity from an originally posterior to an anterior position and at the same time has twisted the visceral commissure.

V. BIONOMICS.

The Gastropoda are essentially aquatic animals, and the more archaic species are marine. Some species are specially adapted to brackish waters. In fresh waters there are found sundry Streptoneura, viz. certain Neritidae, the Ampullariidae, Paludinidae, Valvatidae, Bithyniidae, Hydrobiidae, several Cerithiidae, the Melaniidae, *Cremnoconchus*, and *Canidia*; nearly the whole pulmonate group of Basommatophora; and a single Opisthobranchiate, *Ancylodoris*. Finally, the stylommatophorous Pulmonates and Halicinidae, Cyclophoridae, Cyclostomatidae, and Aciculidae among the Streptoneura are terrestrial. In some forms that live in torrential streams, or are subject to being dried up periodically, the respiration is alternately aquatic and aerial, and the Amphibolidae, Siphonariidae, and Onciidiidae are examples of Pulmonates that have returned to a marine existence. The Gastropoda crawl at the bottom of the water, or on the land, or in a reversed position, on the film of mucus secreted on the surface of the water by the glands of the anterior groove of the foot (Basommatophora, Nudibranchia). The Strombidae are jumpers, and a considerable number of Gastropods are swimmers, *e.g.* the Heteropoda—which swim in a reversed position with the foot upwards—*Janthina* (Fig. 135), the "Pteropoda," *Phyllirhoë*, *Acera* (Fig. 147), etc. Some families both of Streptoneura and Opisthobranchia burrow in mud or sand, *e.g.* the Naticidae, Bullidae, etc. Some genera are more or less sedentary, though able to move from place to place—such are *Patella* and *Bathysciadium*—but others are completely sedentary when adult, and may be fixed either by the substance of their shells—such are *Vermetus* and *Magilus* (the latter inhabits corals)—or by a calcareous plate secreted by the foot, as is the case in *Hipponyx*.

The diet of Gastropoda varies according to the group under consideration. Generally speaking, the carnivorous habit is due to specialisation, often accompanied by the development of a proboscis. Various forms of Gastropods live and feed on colonial invertebrates such as Synascidians, Hydrozoa, Anthozoa, and the like, and to a certain degree mimic these forms. Thus *Ovula* lives on *Gorgonia*, *Pedicularia* on Corallium, *Lamellaria* on *Leptoclinum*, various Nudibranchs on sponges or Hydroids. Some Gastropoda are parasitic, generally in or upon Echinoderms, and belong either to the sub-group Capulidae, in which case they are ectoparasites, and had already acquired this habit in Palaeozoic times (*Platyceras*), or to the "Aglossa," that is to say, to the little group formed by the families Eulimidae (including *Stylifer*, parasitic on Asterids, Echinids, and Crinoids) and Entoconchidae, including *Entosiphon*, *Entocolax*, *Entoconcha*, and *Enteroxenos*, all parasitic in Holothurids.

Some thirty thousand species of Gastropoda have been enumerated, of which twenty thousand belong to the present epoch and are distributed in every region of the globe. Of existing species more than twelve thousand are branchiate forms. Some marine species are found at a depth of over 2500 fathoms, and some Pulmonata live in the Himalayas at a height of nearly 17,000 feet above the level of the sea. Some freshwater Gastropoda (Hydrobiidae, Basommatophora) exist at a depth of 180 fathoms below the surface of certain lakes, *e.g.* Lake Baikal; others live in subterranean waters, and some Pulmonates are found in caverns into which the daylight does not penetrate. Palaeontology shows that these animals were already in existence in the Cambrian period, at the commencement of the Palaeozoic epoch.

The size of Gastropods varies from a fraction of a millimetre to more than fifty centimetres. The largest forms are found not only among the testaceous species, such as *Fusus*, *Tritonium*, *Ancistromesus*, *Strombus*, etc., but also among the naked forms: *Tethys*, for example, is more than thirty centimetres in length, and some species of *Dendronotus* as much as twenty-five centimetres.

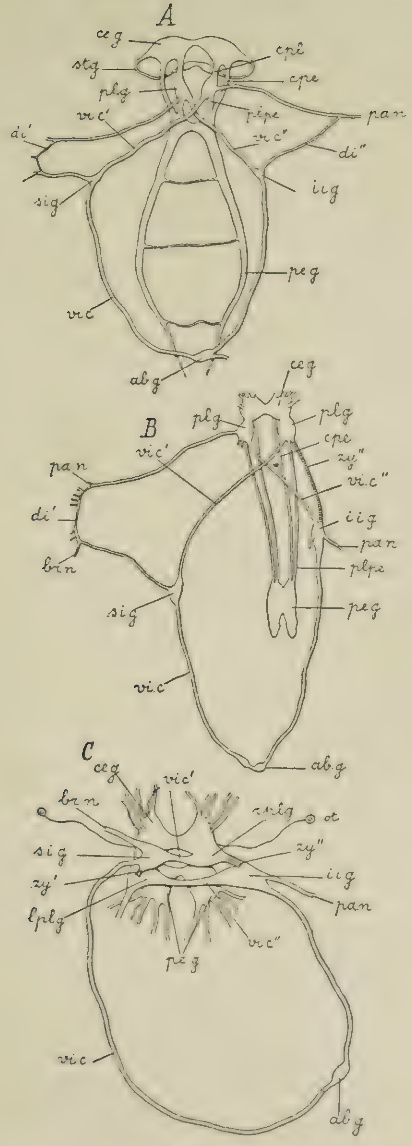
VI. Systematic Review of the Sub-Classes, Orders, and Families of Gastropoda.

The class Gastropoda includes two well-defined sub-classes, Streptoneura and Euthyneura.

Sub-Class I. Streptoneura, Spengel

(= Prosobranchia, Milne-Edwards = Cochlides, von Jhering).

These are dioecious Gastropoda, with the exception of a few aberrant genera, and are characterised by the maximum torsion exhibited by the visceral mass and visceral commissure, the latter being always twisted into a figure of eight (Fig. 124, VII, IX). The right moiety of this commissure is situated above the digestive tube, and is known as the supra-intestinal; the left moiety is situated below the digestive tube, and is known as the infra-intestinal. The pleural ganglia are often united to the opposite branch of the visceral nerve by an anastomosis of the pallial nerve, this condition constituting "dialyneury" (Fig. 123, A, *di′*, *di″*): or there may be a direct connection by means of a longer or shorter connective passing from the pleural ganglion to the ganglion borne on the visceral branch of the opposite side; this constitutes "zygoneury" (Fig. 123, B, C, *zy′*, *zy″*). Zygoneury is more frequently found on the


A
ce.g
cpl
st.g
cpe
pl.g
pl.pe
pan
vi.c'
di'
vi.c''
di''
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si.g
pe.g
vi.c
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B
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cpe
vi.c'
zy''
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zy'
i.i.g
l.pl.g
pan
vi.c''
pe.g
vi.c
ab.g

FIG. 123.

Nervous system of 3 Streptoneurous Gastropods, showing the dialyneury and zygoneury, dorsal aspect. *A*, *Paludina* (after Bouvier, somewhat modified); *B*, *Triton* (after Haller); *C*, *Littorina* (after Bouvier). *ab.g*, abdominal ganglion; *br.n*, branchial nerve; *ce.g*, cerebral ganglion; *c.pe*, cerebro-pedal connective; *c.pl*, cerebro-pleural connective; *di'*, *di''*, left and right dialyneury; *i.i.g*, intra-intestinal ganglion; *ot*, otocyst; *pa.n*, pallial nerve; *pe.g*, pedal ganglion; *pl.g*, pleural ganglion; *pl.pe*, pleuro-pedal connective; *s.i.g*, supra-intestinal ganglion; *st.g*, stomato-gastric ganglion; *vi.c*, visceral commissure; *vi.c'*, *vi.c''*, supra-intestinal and intra-intestinal part of the visceral commissure; *zy'*, *zy''*, left and right zygoneury.

right side; the connective passes from the right pleural to the infra-intestinal ganglion, and may have the effect of bringing the latter ganglion between the two pleural centres (Fig. 123, C, *i.i.g*). The head of Streptoneura bears only a single pair of tentacles (Fig. 125, *a*). The radular teeth, when there is more than one on either side of the median tooth, are of several different kinds in each transverse row (Fig. 74, C, F). The heart is almost always posterior to the branchia. The sub-class includes two orders, Aspidobranchia and Pectinibranchia.

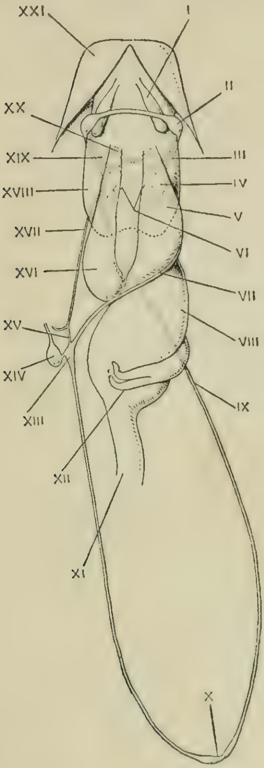

FIG. 124.

Trochus cinerarius, central nervous system, dorsal aspect, with the anterior part of the digestive tract. I, salivary gland; II, cerebral ganglion; III, cerebro-pleural connective; IV, pleural ganglion; V, right pallial nerve; VI, pedal ganglion; VII, supra-intestinal part of the visceral commissure; VIII, posterior part of the glandular oesophagus; IX, infra-intestinal part of the visceral commissure; X, abdominal ganglion; XI, oesophagus; XII, radula; XIII, supra-intestinal ganglion; XIV, osphradial ganglion and branchial nerve; XV, left pallial anastomosis or dialyneury; XVI, glandular oesophagus; XVII, left pallial nerve; XVIII, buccal mass; XIX, cerebro-pedal connective; XX, stomato-gastric ganglion; XXI, snout.

ORDER 1. **Aspidobranchia.**

These are Streptoneura in which the nervous system is still but little concentrated (Fig. 124). The pedal centres have the form of long ganglionated cords, to the anterior end of which the pleural centres are attached: the cerebral ganglia are widely separated from one another, and are united by a long commissure lying in front of the buccal mass and the salivary glands (Fig. 127, *c.c*). An infra-oesophageal or "labial" cerebral commissure is present. The osphradium is but little specialised, and is situated on the branchial nerve. The otocyst contains numerous otoconia. The eye is open (Fig. 100), or if closed has a very small pellucida. The central teeth of the radula are multiplied. Ctenidia are almost always present; they are bipectinate and free at their distal ends (Fig. 81, *d*). As a rule, the Aspidobranchs exhibit well-marked traces of the original bilateral symmetry, having two auricles to the heart and two kidneys (Fig. 127), the last named opening to the exterior at the end of short papillae (Fig. 88, *f*). The gonad has no accessory organs and discharges its products into the right kidney. In the Neritacea, however, there is only one kidney, namely, the left kidney, with a slit-shaped external aperture, and there is a distinct genital orifice, the oviduct being diaulic in the Neritidae.

The order Aspidobranchia includes the most archaic Gastropods: it includes two sub-orders, the Docoglossa and Rhipidoglossa.

Sub-Order 1. Docoglossa.

In these Aspidobranchs the nervous system (Fig. 93) is without dialyneury, that is to say, there is no anastomosis between the pleural ganglia and the visceral nerve of the opposite side through the intermediary of the pallial nerve. The eyes are open and devoid of a crystalline lens. There are two osphradia, but neither hypobranchial glands nor operculum. The mandible is unpaired and dorsal. The radula generally has trabeculiform teeth (Fig. 74, F), and there are at most three marginal teeth on either side. The heart has only a single auricle (Fig. 82, *au*), and neither it nor the pericardium are traversed by the rectum. The visceral mass is cone-shaped, without a spire. The sub-order includes about 1400 species.

Family 1. Acmaeidae, Philippi. A single bipectinate ctenidium, free for the greater part of its extent, is present on the left side (Fig. 82). Genera—*Acmaea*, Eschsholtz; without pallial branchiae; Great Britain. *Scurria*, Gray; with pallial branchiae arranged in a circle beneath the mantle. *Pectinodonta*, Dall. *Scenella*, Billings; from the Cambrian. *Palaeacma*, Hall; from the Silurian. Family 2. Tryblidiidae, Pilsbry. Muscle scar divided into numerous separate impressions. Genus—*Tryblidium*, Lindström; Silurian. Family 3. Patellidae, Guilding. No ctenidia, but only pallial branchiae disposed in a circle between the mantle and the foot (Fig. 125). Genera—*Patella*, Linnaeus; the pallial branchiae forming a complete circle; no epipodial tubercles; British seas. *Ancistromesus*, Dall: radula with an unpaired central tooth, which is wanting in *Patella*. *Nacella*, Schumacher; branchial circle complete; epipodial tentacles present. *Helcion*, Montfort; circlet of pallial branchiae interrupted anteriorly, beneath the head; British seas. *Helcioniscus*, Dall. Family 4. Lepetidae, Gray. Dioecious, with otoconia; the head symmetrical, the foot elongated; neither ctenidia nor pallial branchiae present; a central tooth in the radula. Genera—*Lepeta*, Gray; without eyes. *Lepetella*, Verrill; with eyes. *Pilidium*, Forbes. *Propilidium*, Forbes and Hanley. Family 5. Bathysciadidae, Dautzenberg and Fischer. Monoecious, with otoliths; head provided with an appendage on the right side; radula without a central tooth. Genus—*Bathysciadium*, Dautzenberg and Fischer; abyssal (Fig. 126).

Sub-Order 2. Rhipidoglossa.

Aspidobranchia with a dialyneurous nerve-system, that is to say, with a pallio-visceral anastomosis (Fig. 124, XV); eyes with a crystalline lens (Fig. 100, 1); a single osphradium, except in genera with two ctenidia; one or two hypobranchial glands. Mandibles paired, lateral. Radula with very numerous marginal teeth, arranged like the sticks of a fan.

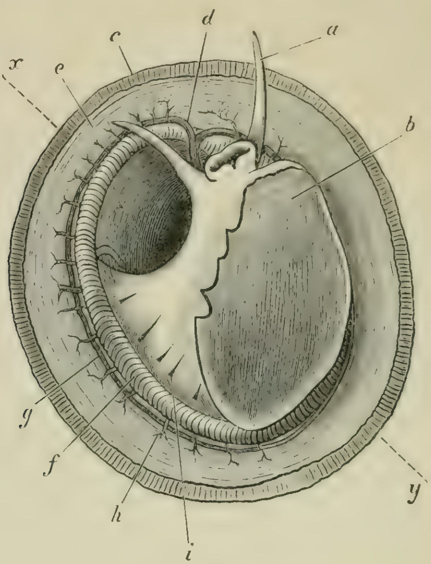

FIG. 125.

Patella vulgata, in its shell, seen from the pedal surface; *x*, *y*, the median antero-posterior axis. *a*, cephalic tentacle; *b*, plantar surface of the foot; *c*, free edge of the shell; *d*, the branchial efferent vessel carrying aerated blood to the auricle, and here interrupting the circlet of gill lamellae; *e*, margin of the mantle-skirt; *f*, gill lamellae—special pallial outgrowths (not ctenidia); *g*, the branchial efferent vessel; *h*, factor of the branchial advehent vessel; *i*, interspaces between the muscular bundles of the root of the foot. (After Lankester.)

Oesophagus with a frill, oesophageal glands (Fig. 124, XVI), and a stomachal caecum, often coiled in a spiral (Fig. 127, *sp.c*). Heart with two auricles; ventricle traversed by the rectum (Fig. 55) except in the Helicinidae, in which there is only a single auricle and the rectum only passes through the pericardium. An epipodial ridge on each side of the foot (Fig. 130, VIII), and cephalic expansions between the tentacles often present.

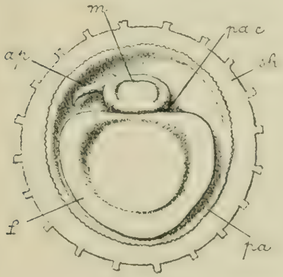

FIG. 126.

Bathysciadium, ventral aspect, magnified. *ap*, cephalic appendage; *f*, foot; *m*, mouth; *pa*, mantle; *pa.c*, pallial cavity; *sh*, shell.

FAMILY 1. PLEUROTOMARIIDAE. Visceral mass and shell spiral; mantle and shell with an anterior fissure (Fig. 54, III) near the median line. Two ctenidia; a horny operculum. Genera—*Pleurotomaria*, Defrance; epipodium without tentacles; two bipectinate ctenidia (Fig. 127). Five living species from the Antilles, Japan, and the Moluccas. The first recent species (*P. quoyana*, Crosse and Fischer) was discovered in 1856; the animal was first obtained in 1871, in a collection made off the Barbadoes by the "Hassler" (A. Agassiz). The Moluccan species is nineteen centimetres in height. The genus includes several hundred extinct species, ranging from the Silurian to the Tertiary, but is rare in the last named. *Scissurella*, d'Orbigny ; epipodium with tentacles ; right ctenidium monopectinate (Fig. 128). *Schismope*, Jeffreys ; the slit at the margin of the shell is closed in the adult and transformed into an orifice (Fig. 62). The following genera are exclusively fossil : *Porcellia*, Léveillé ; Devonian and Carboniferous. *Kokenella*, Kittl ; Trias. *Ditremaria*, d'Orbigny ; Jurassic. *Polytremaria*, de Koninck ; Carboniferous. *Trochotoma*, Deslongchamps ; Trias and Jurassic. *Cantantostoma*, Sandberger ; Devonian. *Murchisonia*, d'Archiac and Verneuil ; Cambrian to Trias. *Odontomaria*, Roemer ; Devonian. FAMILY 2. BELLEROPHONTIDAE, MacCoy. An exclusively fossil family, comprising more than 300 species extending from the Cambrian to the Trias. The shell is coiled in one plane and has an incision in the mid-dorsal margin of the aperture. Genera—*Bellerophon*, Montfort. *Euphemus*, MacCoy. *Salpingostoma*, Roemer. *Trematonotus*, Hall. *Cyrtolites*, Conrad. FAMILY 3. EUOMPHALIDAE, de Koninck. Also an extinct family, extending from the Cambrian to the Cretaceous. Spire slightly prominent ; umbilicus deep ; operculum calcareous. Genera—*Euomphalus*, Sowerby. *Straparollina*, Billings. *Ophileta*, Vanuxem. *Maclurea*, Lesueur. *Platychisma*, MacCoy. *Straparollus*, Montfort. *Phanerotinus*, Sowerby. *Discohelix*,

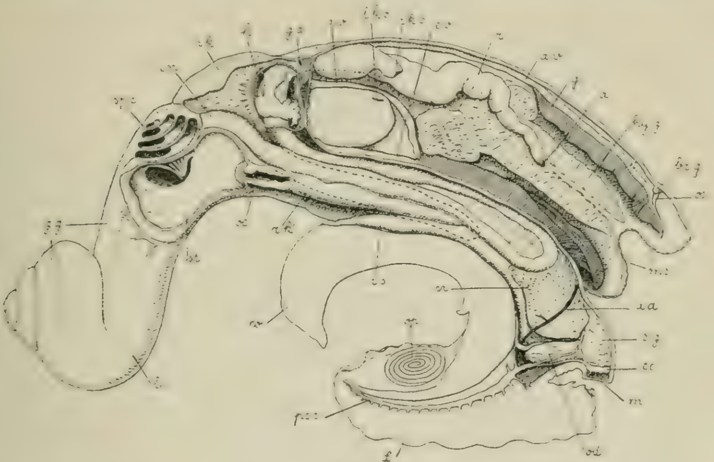

FIG. 127.

Pleurotomaria, with the pallial cavity laid open, right-side view. *a*, anus ; *aa*, aorta ; *a.v*, afferent branchial vessel ; *br.g*, branchial ganglion ; *c.c*, cerebral commissure ; *co*, columellar muscle ; *cr*, crop ; *e.v*, efferent branchial vessel ; *f*, foot ; *g*, right or minor gill ; *g.d*, genital duct ; *gg*, gonad ; *h*, heart in the pericardium ; *hy.g*, hypobranchial gland ; *in*, intestine ; *li*, liver ; *l.k.o*, opening of the left kidney ; *m*, mouth ; *m.s*, mantle slit ; *od*, odontophore ; *oe*, oesophagus ; *op*, operculum ; *os*, osphradium ; *pe.c*, pedal cord ; *r*, rectum ; *r.k*, right kidney ; *r.k'*, anterior part of ditto (dotted line) ; *r.k.o*, opening of the right kidney ; *r.s*, radular sac ; *s.g*, salivary gland ; *sp.c*, spiral caecum ; *st*, stomach. (After F. M. Woodward.)

Dunker. Family 4. Haliotidae, Fleming. Spire of the visceral mass and shell much reduced; two bipectinate ctenidia, the right being the smaller; no operculum. Genus—*Haliotis*, Linnaeus (Fig. 129). Family 5. Velainiellidae, Vasseur. An extinct family from the Eocene. Shell elongate, with numerous whorls; columella and partitions between the whorls absent; internal cavity open from base to summit. Genus, *Velainiella*, Vasseur. Family 6. Fissurellidae, Risso. Visceral mass and shell conical; the anterior part of the mantle exhibits a slit or a hole in the median line; two symmetrical ctenidia; no operculum.

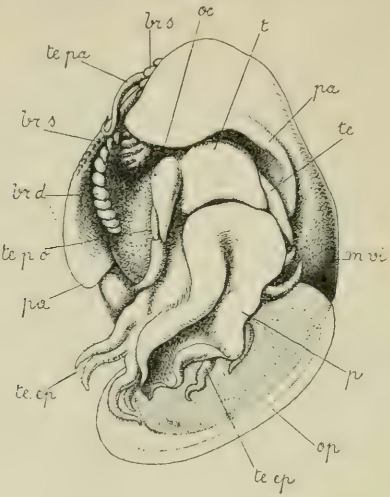

Fig. 128.

Scissurella euglypta, removed from its shell; ventral aspect, magnified. *br.d*, right gill; *br.s*, left gill; *m.vi*, visceral mass; *oc*, right eye; *op*, operculum; *p*, foot; *pa*, mantle; *t*, snout; *te*, left cephalic tentacle; *te.ep*, epipodial tentacles; *te.pa*, pallial tentacle; *te.p.o*, post-ocular tentacle.

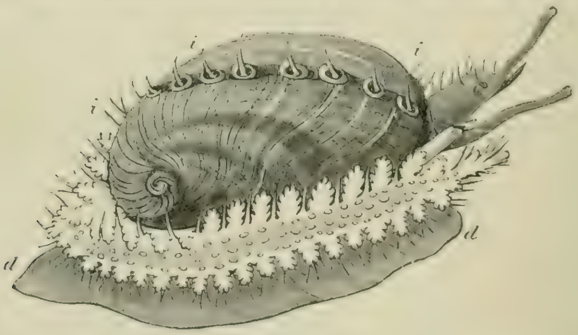

Fig. 129.

Haliotis tuberculata, right-side view. *d*, foot; *i*, tentacular process of the mantle, passing through the shell-foramina. (From Lankester, after Cuvier.)

Genera — *Emarginula*, Lamarck; anterior border of the mantle and shell with a slit; British seas. *Rimula*, Defrance. *Subemarginula*, Blainville. *Scutum*, Montfort; mantle split anteriorly and partially reflected over the shell, which has no anterior slit. *Zeidora*, Adams. *Puncturella*, Lowe; mantle and shell with a foramen in front of the summit of the visceral cone; British. *Fissurella*, Bruguière; mantle and shell perforated by a hole at the summit of the visceral cone, the hole leading into the branchial chamber; British. *Glyphis*, Carpenter. *Fissurellidea*, d'Orbigny. *Pupillia*, Gray; mantle completely covering the shell. *Lucapina*, Gray. *Megatebennus*, Pilsbry. *Macrochisma*, Swainson. *Lucapinella*, Pilsbry. Family 7. Cocculinidae, Dall. Shell conical, symmetrical, without slit or perforation; the summit inclined backwards. Genus — *Cocculina*, Dall; dioecious; abyssal. Family 8. Trochidae, d'Orbigny. Visceral mass and shell spirally coiled; a single ctenidium; eyes open (Fig. 100); a horny operculum; flattened lobes between the tentacles (Fig. 130, II). Genera—*Trochus*, Linnaeus; no jaws; shell umbilicated; spire pointed and prominent. *Monodonta*, Lamarck; no jaws; spire not prominent; no umbilicus; columella toothed. *Clanculus*, Montfort. *Elenchus*, Swainson. *Photinula*, Adams. *Gaza*, Watson. *Gibbula*, Risso; with jaws; three pairs of epipodial cirrhi without pigment spots at their bases (Fig. 130); British. *Margarita*, Leach; from five to seven pairs of epipodial tentacles with a pigment spot at the base of each. *Livona*, Gray. *Basilissa*, Watson. Family 9. Stomatellidae, Gray. Spire of the visceral mass and shell much reduced; a single ctenidium. Genera — *Stomatella*, Lamarck; foot truncated posteriorly; an operculum present; no epipodial tentacles. *Gena*, Gray; foot elongated posteriorly; no operculum; epipodial tentacles present. *Stomatia*, Helbling; foot not truncated; operculum and epipodial tentacles absent. Family 10. Delphinulidae, Fischer. Visceral mass and shell spirally coiled; operculum horny; in-

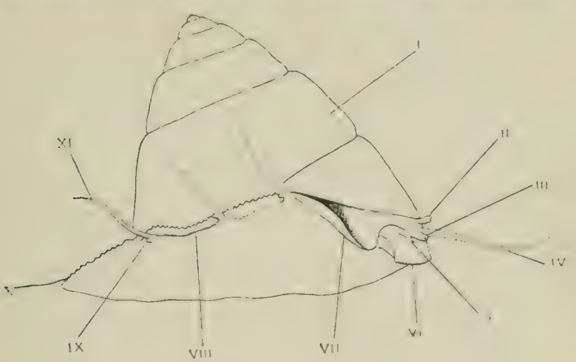

Fig. 130.

Trochus (*Gibbula*) *cinerarius*, right-side view. I, shell; II, frontal lobes; III, right eye and peduncle; IV, right tentacle; V, appendage of the right ocular peduncle; VI, snout; VII, right epipodial lobe; VIII, epipodium; IX, claviform appendage under the epipodial tentacle; X, posterior (operculigerous) part of the foot; XI, epipodial tentacle.

tertentacular lobes absent. Genus—*Delphinula*, Lamarck; with five pairs of epipodial tentacles. Family 11. Liotiidae, Gray. Shell globular; margin of aperture thickened; operculum horny, with a calcareous layer. Genus—*Liotia*, Gray. Family 12. Cyclostrematidae, Fischer. Shell flattened, umbilicated, not nacreous; foot truncated anteriorly and with the two angles prolonged into tentacles. Genera—*Cyclostrema*, Marryat (Fam. 50). *Teinostoma*, Adams. Family 13. Trochonematidae, Zittel. Exclusively fossil, from Cambrian to Cretaceous; shell spiral and nacreous internally; whorls without keels; aperture rounded. Genera—*Trochonema*, Salter; from the Cambrian and Silurian. *Eunema*, Salter; from the Ordovician to the Devonian. *Amberleya*, Morris and Lycett; from the Trias to the Cretaceous. *Oncospira*, Zittel; Jurassic. Family 14. Turbinidae, Gray. Visceral mass and shell spirally coiled; epipodial tentacles present; eyes closed; operculum calcareous and thick. Genera—*Turbo*, Linnaeus; shell globular, thick, with short spire. *Astralium*, Link. *Mölleria*, Jeffreys; shell thin, umbilicated, with very short spire. *Cyclonema*, Hall. Family 15. Phasianellidae, Troschel. Shell not nacreous, without umbilicus, with prominent spire and polished surface. Genus—*Phasianella*, Lamarck. Family 16. Umboniidae, Adams. Shell flattened, not umbilicated, generally smooth, without a nacreous layer; operculum horny. Genera—*Umbonium*, Link. *Isanda*, Adams. Family 17. Neritopsidae, Fischer. Shell semiglobular, with short spire; operculum calcareous, not spiral. Genera—*Neritopsis*, Grateloup. *Naticopsis*, MacCoy; from the Devonian to the Trias. Family 18. Macluritidae, Fischer. Shell discoid, deeply umbilicated, with few whorls; operculum spiral, thick. Genus—*Maclurites*, Lesueur; from Cambrian and Silurian. Family 19. Neritidae, Lamarck. Shell with very low spire; without umbilicus and without a nacreous layer; internal partitions frequently absorbed; operculum calcareous, provided with an apophysis; epipodium slightly developed, without tentacles; a single ctenidium; a cephalic penis present. Genera—*Nerita*, Adanson; marine. *Neritina*, Lamarck; freshwater; British. *Neritodomus*, Morris and Lycett; Jurassic. *Deianira*, Stoliczka; Cretaceous. *Septaria*, Férussac; shell boat-shaped, with a large aperture and symmetrical muscular impressions. *Pileolus*, Sowerby; from the Jurassic and Cretaceous. Family 20. Titiscaniidae, Bergh. Without shell and operculum, but with a pallial cavity and a ctenidium. Genus—*Titiscania*, Bergh (Fig. 131); from the Pacific Ocean. Family 21. Helicinidae, Pfeiffer. No ctenidium, but a pulmonary cavity present; epipodium without tentacles; heart with a single auricle, and not traversed by the rectum; no mandible; operculum without apophyses. Genera—*Helicina*, Lamarck. *Eutrochatella*, Fischer. *Stoastoma*, Adams. *Bourcieria*, Pfeiffer. Family 22. Hydrocenidae, Fischer. No ctenidium, but a pulmonary cavity present; foot obtuse; operculum calcareous, with an

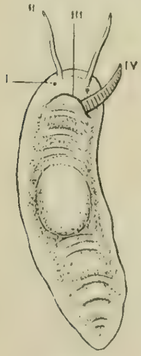

Fig. 131.

Titiscania limacina, dorsal aspect. I, eye; II, tentacle; III, opening of the pallial cavity; IV, gill. (After Bergh.)

apophysis. Genus—*Hydrocena*, Parreys; from Dalmatia. Family 23. Proserpinidae, Fischer. Differs from the two last families in not having an operculum. Genus—*Proserpina*, Gray; from Central America.

Order 2. **Pectinibranchia.**

These are Streptoneura with a somewhat concentrated nervous system: without a labial commissure, except in *Paludina* and *Ampullaria*. The nerve-collar is situated behind the buccal bulb, except in *Ampullaria*. There is a single well-differentiated, independent, and often pectinated osphradium. The eye is always closed, and the internal cornea (pellucida) is extensive. Each otocyst contains a single otolith, except in some forms of Taenioglossa devoid of a proboscis, *e.g. Paludina*, *Valvata*, *Ampullaria*, *Cyclophorus*, *Typhobia*, *Bythoceras*, *Nassopsis*, certain Cerithiidae, etc. The central tooth of the radula is single or absent. There is no longer any trace of bilateral symmetry in the circulatory, respiratory, and excretory organs, the topographically right half of the pallial complex having completely disappeared. The heart has only a single auricle—that of the morphologically right side—and is not traversed by the rectum. The ctenidium is monopectinate and attached to the mantle throughout its length, except in *Adeorbis* and *Valvata*, the latter genus being the only Pectinibranch with a bipectinate ctenidium. The single kidney usually opens directly by a slit-shaped aperture (but exceptionally by a ureter in *Paludina*, *Cyclophorus*, and *Valvata*), and never serves for the passage of the sexual products. The gonad always has a separate orifice of its own. The male generally has a penis (Fig. 44, A, *h*).

The Pectinibranchia are divided into two sub-orders—Taenioglossa and Stenoglossa.

Sub-Order 1. Taenioglossa.

In these Pectinibranchs the radula has normally three teeth on each side of the median tooth, viz. one lateral and two marginals (Fig. 2, B; 74, B). The stomatogastric ganglia are situated behind the buccal mass, and are united to the cerebral centres by long connectives which are in part recurrent and deeply situated. The salivary ducts, when sufficiently long, traverse the nerve-collar. The oesophagus is nearly always devoid of an unpaired gland. Usually there is neither a proboscis nor a siphon. The sub-order includes two distinct groups or tribes, which are respectively creeping and swimming forms, namely, the Platypoda and Heteropoda.

Tribe 1. Platypoda.

Normal Taenioglossa, but slightly modified, and of creeping habit. The foot is flattened ventrally, at all events in its anterior part (Strombidae). The otocysts are situated close to the pedal nerve-centres. Accessory organs are rarely found on the genital ducts, but are present in *Paludina*, *Cyclostoma*, the Naticidae, Calyptraeidae, etc. Mandibles are usually present. The intestine is long. The Platypoda form the largest group of the Mollusca, comprising nearly sixty families of unequal value, some of which are not thoroughly well known from an anatomical point of view.

FAMILY 1. PALUDINIDAE, d'Orbigny. Ctenidium monopectinate; pedal centres in the form of ganglionated cords; the kidney is provided with a ureter; viviparous; fluviatile. Genera—*Paludina*, Lamarck. *Neothauma*, Smith; from Lake Tanganyika. *Tylopoma*, Brusina; from the Tertiary. FAMILY 2. CYCLOPHORIDAE, Gray. Pallial cavity devoid of a ctenidium and transformed into a lung; pedal centres in the form of ganglionated cords; otocysts with otoconia; aperture of the shell and the operculum circular; terrestrial. Genera—*Pomatias*, Hartmann; shell turriculated. *Diplommatina*, Benson. *Hybocystis*, Benson. *Cyclophorus*, Montfort; shell umbilicated, with a short spire and horny operculum. *Cyclosurus*, Morelet; shell uncoiled. *Dermatocera*, Adams; foot provided with a horn-shaped protuberance at its posterior end. *Spiraculum*, Pearson; aperture provided with a sutural tube at its superior angle. FAMILY 3. AMPULLARIIDAE, Gray. A monopectinate ctenidium present, and to the left of it a pulmonary sac, separated from the ctenidium by an incomplete septum; oesophageal nerve-collar in front of the buccal bulb; penis pallial; amphibious. Genera — *Ampullaria*, Lamarck; visceral sac and shell coiled dextrally. *Lanistes*, Montfort; shell sinistral; spire short or obsolete. *Meladomus*, Swainson; shell elongated, sinistral. FAMILY 4. LITTORINIDAE, Gray. Ctenidium monopectinate; oesophageal pouches present; pedal nerve-centres concentrated; a pedal penis near the right tentacle. Genera—*Littorina*, Férussac; shell not umbilicated; foot devoid of appendages; marine forms of semi-aerial habit (Fig. 85). *Lacuna*, Turton; foot with two posterior appendages; marine forms of exclusively aquatic habit (Fig. 7). *Cremnoconchus*, Blandford; shell umbilicated; of exclusively aerial habit; Indian. *Risella*, Gray. *Tectarius*, Valenciennes. FAMILY 5. FOSSARIDAE, Fischer. Shell turbinated and umbilicated; head with two cephalic lobes, as in some Rhipidoglossa. Genus—*Fossarus*, Philippi. FAMILY 6. PURPURINIDAE, Zittel. An exclusively fossil family; shell thick, with prominent spire, angular whorls, and oval aperture. Genera — *Purpurina*, d'Orbigny; Jurassic. *Brachytrema*, Morris and Lycett; Jurassic. *Scalites*, Conrad; Ordovician. FAMILY 7. PLANAXIDAE, Adams. Shell not umbilicated, with pointed spire; the external border of the shell sharp; a short pallial siphon. Genus — *Planaxis*, Lamarck. FAMILY 8. CYCLOSTOMATIDAE, Pfeiffer. Pallial cavity transformed into a lung; pedal centres concentrated; otocysts with otoliths; no mandibles; a deep longitudinal pedal groove present; terrestrial. Genera—*Cyclostoma*, Draparnaud; shell turbinated; operculum calcareous; British. *Omphalotropis*, Pfeiffer; shell turriculated; operculum horny. FAMILY 9. ACICULIDAE, Gray. Shell narrow and elongated; operculum horny; pallial cavity a pulmonary chamber; otocysts with otoconia. Genus — *Acicula*, Hartmann. FAMILY 10. VALVATIDAE, Gray. Ctenidium bipectinate, free throughout its length; a pallial filament on the right side; hermaphrodite; fluviatile. Genus—

Valvata, Müller (Fig. 132); British. Family 11. Rissoidae, Gray. A monopectinate ctenidium; epipodial filaments present; one or two pallial tentacles; snout elongated. Genera — *Rissoa*, Fréminville; operculum simple. *Rissoina*, d'Orbigny; operculum with an apophysis. *Stiva*, Hedley. Family 12. Litiopidae, Fischer. Foot with an epipodium bearing three pairs of tentacles and an operculigerous lobe with two appendages; inhabitants of the Sargasso weed. Genus—*Litiopa*, Rang. Family 13. Adeorbiidae, Fischer. Mantle with two posterior appendages; ctenidium large and capable of being protruded from the pallial cavity; shell depressed and umbilicated. Genus—*Adeorbis*, Wood; British (Fig. 133). Family 14. Jeffreysiidae, Fischer. Head with two long labial palps; shell ovoid, umbilicated; operculum horny, semicircular, concentric, and carinated. Genus—*Jeffreysia*, Alder. Family 15. Homalogyridae, Sars. Shell flattened; operculum horny, circular; no cephalic tentacles.

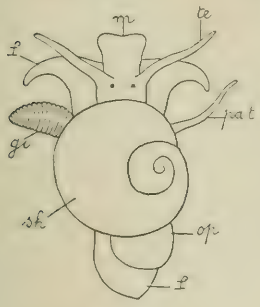

Fig. 132.

Valvata piscinalis, dorsal aspect, magnified. *f*, foot; *gi*, gill; *m*, mouth; *op*, operculum; *pa.t*, pallial tentacle; *sh*, shell; *te*, cephalic tentacle. (After Bernard.)

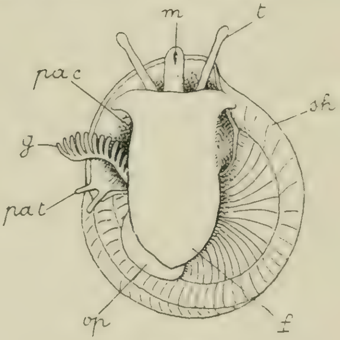

Fig. 133.

Adeorbis subcarinatus, ventral aspect. *f*, foot; *g*, gill; *m*, mouth; *op*, operculum; *pa.c*, pallial cavity; *pa.t*, pallial tentacle; *sh*, shell; *t*, tentacle. (After F. M. Woodward.)

Genera—*Homalogyra*, Jeffreys; British. *Ammonicera*, Vayssière. Family 16. Skeneidae, Fischer. Shell depressed and umbilicated, with a rounded aperture; cephalic tentacles long. Genus—*Skenea*, Fleming; British. Family 17. Choristidae, Fischer. Shell spiral; four cephalic tentacles; eyes absent; two pedal appendages behind the operculum. Genus—*Choristes*, Verrill. Family 18. Assimineidae, Fischer. Shell conical, with a short spire; operculum horny, spiral; eyes situated at the free extremities of the tentacles. Genus—*Assiminea*, Leach; estuarine; British. Family 19. Truncatellidae, Gray. Ctenidium monopectinate; snout very long, bilobed; foot very short; spire elongated and truncated; marine and littoral. Genus—*Truncatella*, Risso. Family 20. Hydrobiidae, Fischer. Shell with prominent spire; ctenidium monopectinate; sexes separate; penis distant from the right tentacle and generally appendiculated; otocysts with otoliths; brackish water or fluviatile. Genera—*Hydrobia*, Hartmann; shell conical, smooth with scarcely convex whorls; operculum horny; brackish water; British. *Baikalia*, von Martens; from Lake Baikal. *Pomatiopsis*, Tryon; foot divided into two sections by a transverse furrow; penis without an appendage. *Bithynella*, Moquin-Tandon. *Lithoglyphus*, Mühlfeldt; shell globular with short spire. *Spekia*, Crosse; viviparous; from Lake Tanganyika. *Tanganyicia*, Crosse (Fig. 78). *Limnotrochus*, Smith; from Lake Tanganyika. *Chytra*, Moore. *Littorinida*, Eydoux and Souleyet. *Bithynia*, Gray; shell conical with an oval aperture; operculum calcareous, concentric; habitat fluviatile; British. *Stenothyra*, Benson; aperture rounded and contracted; operculum calcareous, spiral. FAMILY 21. MELANIIDAE, Gray. Shell spiral, the spire somewhat elongated; operculum horny; foot and snout short; mantle border fringed; viviparous (Fig. 109); fluviatile. Genera—*Melania*, Lamarck; shell turriculated; aperture rounded and enlarged anteriorly. *Faunus*, Montfort; spire very long; aperture of shell notched anteriorly. *Paludomus*, Swainson; shell short, thick, with rounded aperture. *Melanopsis*, Férussac. *Nassopsis*, Smith. *Bythoceras*, Moore; from Lake Tanganyika. FAMILY 22. TYPHOBIIDAE, Moore. Foot wide; tentacles elongate; shell turriculated, with carinated whorls, the carinae tuberculated or spiny. Genera—*Typhobia*, Smith. *Bathanalia*, Moore; from Lake Tanganyika. FAMILY 23. PLEUROCERIDAE, Fischer. Like the Melaniidae, but the border of the mantle is not fringed and the reproduction is oviparous. Genera—*Pleurocera*, Rafinesque; shell elongated; the aperture canaliculated anteriorly. *Anculotus*, Say; shell short, globular; the aperture rounded anteriorly. FAMILY 24. PSEUDOMELANIIDAE, Fischer. An exclusively fossil family; shell turriculated, with prominent spire and elongated oval aperture. Genera—*Pseudomelania*, Pictet and Campiche; Secondary and Tertiary. *Loxonema*, Phillips; Palaeozoic. *Macrochilus*, Phillips; Devonian to Trias. FAMILY 25. SUBULITIDAE, Fischer. An exclusively fossil family; shell turriculated with a narrow aperture, elongated and canaliculated anteriorly. Genera—*Subulites*, Conrad; Cambrian to Carboniferous. *Fusispira*, Hall; Ordovician. *Euchrysalis*, Laube; Trias. FAMILY 26. NERINEIDAE, Zittel. An exclusively fossil family; shell with numerous whorls, with multiple folds in the lumen of the whorls. Genera—*Nerinea*, Defrance; Jurassic and Cretaceous. *Aptyxiella*, Fischer; Trias and Jurassic. *Ptygmatis*, Sharpe; Jurassic and Cretaceous. FAMILY 27. CERITHIIDAE, Fleming. Shell with elongated spire and numerous tuberculated whorls; aperture canaliculated anteriorly; snout long; pallial siphon short. Genera—*Cerithium*, Adanson; aperture oval; operculum oval, with submarginal nucleus. *Bittium*, Gray; operculum circular, with central nucleus; siphon rudimentary. *Potamides*, Brongniart; eyes situated above the bases of the tentacles; ctenidium rudimentary; brackish water. *Triforis*, Deshayes; shell sinistral. *Lacocochlis*, Dunker and Metzger. *Cerithiopsis*, Forbes and Hanley. FAMILY 28. MODULIDAE, Fischer. This family differs from the Cerithiidae in having a shell with a short spire, without a siphon; the eyes are placed midway up the tentacles. Genus—*Modulus*, Gray. FAMILY 29. VERMETIDAE, d'Orbigny. The animal is fixed by the shell, the last whorls of which are not in contact with one another; foot small, discoidal, with two anterior pedal tentacles, one on each side of the supra-pedal gland. Genera—*Vermetus*, Adanson; shell without a notch on the exterior border of the aperture;

mantle slit in the female only (Fig. 45); pedal tentacles elongate. *Siliquaria*, Bruguière; mantle and shell slit in both sexes for the whole length of the branchial cavity; pedal tentacles rudimentary. Family 30. Caecidae, Gray. Shell almost completely uncoiled in one plane, and furnished with internal septa; aperture circular. Genus—*Caecum*, Fleming (Fig. 68); British. Family 31. Turritellidae, Clark. Shell very long with numerous whorls; head large and prominent; mantle border fringed; no siphon; foot broad and truncated. Genera—*Turritella*, Lamarck; British. *Mesalia*, Gray. *Mathilda*, Semper; the summit of the shell hyperstrophic. Family 32. Struthiolariidae, Fischer. Spire of shell conical; aperture pointed and subcanaliculated anteriorly; foot oval, rather small; head elongate with short tentacles; siphon very slightly developed. Genus—*Struthiolaria*, Lamarck. Family 33. Chenopodidae, Fischer. Spire of shell elongated; margin of aperture expanded; foot elongated and narrow; snout short; tentacles long; siphon very short. Genera—*Chenopus*, Philippi; British. *Alaria*, Morris and Lycett; Jurassic and Cretaceous. *Spinigera*, d'Orbigny; Jurassic. *Diartema*, Piette; Jurassic. Family 34. Strombidae, Gray. Foot narrow, arcuate, compressed laterally, without ventral sole (Fig. 75, *f*); snout long; ocular peduncles longer and stouter than the tentacles. Genera—*Strombus*, Linnaeus; shell ovoid, with elongated aperture; mantle border and aperture of shell not digitate. *Pteroceras*, Linnaeus; mantle border and aperture of shell digitate. *Rostellaria*, Lamarck; spire of shell elongate; aperture prolonged anteriorly into a canal and laterally into an aliform expansion (Fig. 46). *Terebellum*, Klein; shell elongated with a short spire; tentacles aborted. Family 35. Xenophoridae, Philippi. Snout elongated; foot divided transversely into two parts, the posterior part bearing the operculum; shell conical, carinated. Genera—*Xenophorus*, Fischer (Fig. 134); with foreign substances agglutinated on the shell. *Eotrochus*, Whitfield; from the Silurian. Family 36. Capulidae, Fleming. Visceral sac and shell conical, but slightly incurved posteriorly; a tongue-shaped projection between snout and foot; columellar muscle horseshoe-shaped. Genera—*Capulus*, Montfort. *Thyca*, Adams; parasitic on Asterids; without a radula; foot rudimentary. *Platyceras*, Conrad; from the Silurian onwards. Family 37. Hipponycidae, Fischer. Visceral mass and shell conical; foot feebly muscular, capable of secreting a ventral calcareous plate; animal fixed. Genera—*Hipponyx*, Defrance. *Mitrularia*, Schumacher; the shell with an internal appendage shaped like a half-horn. Family 38. Calyptraeidae, Broderip. Visceral mass spiral; shell flattened, with a short spire; lateral cervical lobes present; foot short and circular; accessory genital glands present. Genera—*Calyptraea*, Lamarck; shell spiral, with central summit and circular aperture; British. *Crepidula*, Lamarck; shell oval, with nearly obsolete spire and marginal summit, furnished with an internal horizontal posterior septum. *Crucibulum*, Schumacher; shell conical, with an internal corniform appendage (Fig. 69). Family 39. Naricidae, Recluz. Foot divided into two, the posterior half bearing the operculum; a wide epipodial velum; tentacles flattened; snout elongate; shell turbinated. Genus—*Narica*, Recluz. Family 40. Naticidae, Swainson. Foot highly developed and provided with an aquiferous system; propodium reflected over the head; eyes deeply seated or absent; operculum spiral; burrowing animals. Genera —*Natica*, Adanson; shell globular, thick and polished, umbilicated, with a semi-lunar aperture (Fig. 47); British. *Amaura*, Möller; shell not umbilicated, thin, with an oblong aperture. *Sigaretus*, Lamarck; shell auriform, with a very short spire and large aperture; operculum small and rostrate. FAMILY 41. LAMELLARIIDAE, d'Orbigny. Shell thin, more or less covered by the mantle, and with a small spire; no operculum or propodium; mandibles fused dorsally. Genera—*Velutina*, Fleming; shell only partially covered by mantle; British. *Lamellaria*, Montagu; shell internal, spiral, transparent; British. *Marsenina*, Gray; shell not completely covered by the mantle; hermaphrodite. *Oncidiopsis*, Beck; shell internal, membranous, without spiral; hermaphrodite. FAMILY 42. TRICHOTROPIDAE, Gray. Shell with short spire, umbilicated, carinate and pointed. Genus—*Trichotropis*, Broderip and Sowerby. FAMILY 43. SEGVENZIIDAE, Verrill. Shell trochiform, with canaliculated aperture and twisted columella; operculum spiral. Genus—*Seguenzia*, Jeffreys; abyssal. FAMILY 44. JANTHINIDAE. Shell thin; operculum absent; tentacles bifid; eyes absent; foot short, provided with an epipodium and secretes a float; radula with similar pointed teeth (Fig. 74, D); pelagic. Genera—*Janthina*, Lamarck; shell blue, with a short spire; ctenidium with long pointed filaments, capable of being protruded from the pallial cavity (Fig. 135). *Recluzia*, Petit; shell white with elongated spire. FAMILY 45. CYPRAEIDAE, Fleming. Shell inrolled, solid, polished, the spire nearly hidden, the aperture very narrow in the adult; pallial aperture provided with a short anterior siphon; a short proboscis; anus posterior; foot broad; osphradium with three lobes; mantle reflected

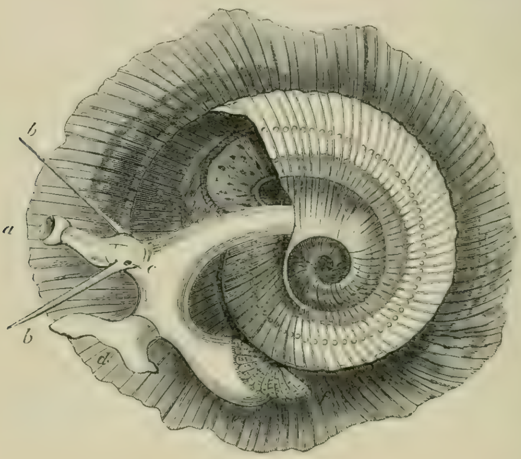

FIG. 134.

Xenophorus exutus, animal and shell, left-side view. *a*, snout; *b*, cephalic tentacles; *c*, left eye; *d*, anterior part of the foot (to the right of this is seen the posterior lobe of the foot bearing the sculptured operculum *f*). (From Lankester, after Owen.)

over the shell (Fig. 70). Genera—*Cypraea*, Linnaeus; shell ventricose with a crenelated columella. *Pustularia*, Swainson; differs from *Cypraea* in having an internal shell. *Ovula*, Bruguière; columella smooth, both ends of the aperture canaliculated (Fig. 136). *Pedicularia*, Swainson; attached to corals; foot small; shell irregular with an expanded aperture. *Erato*, Risso; shell piriform, with a prominent spire. FAMILY 46. TRITONIDAE, Adams. Shell turriculated and siphonated, thick, each whorl of the spire provided with varices; foot broad and truncated anteriorly; pallial siphon well developed; a proboscis. Genera—*Triton*, Montfort; varices not continuous from one whorl to another; eyes at the bases of the tentacles (Fig. 44, A). *Persona*, Montfort; whorls irregular; eyes half-way up the tentacles. *Ranella*, Lamarck; varices continuous from one whorl to another. FAMILY 47. COLUMBELLINIDAE, Fischer. An exclusively fossil family; shell with prominent spire, narrow aperture, and callous columella. Genera—*Columbellina*, d'Orbigny; cretaceous. *Columbellaria*, Rolle; Jurassic. *Zittelia*, Gemellaro; Jurassic. *Petersia*, Gemellaro; Jurassic. FAMILY 48. CASSIDIDAE, Adams. Shell ventricose, with elongated aperture and short spire; foot broad and rounded anteriorly; proboscis and siphon long; operculum with marginal nucleus. Genera—*Cassis*, Lamarck; shell varicose, with narrow aperture. *Cassidaria*, Lamarck; shell without varices, aperture oval and canaliculated. *Oniscia*, Sowerby; shell oval, with a linear aperture. FAMILY 49. OOCORYTHIDAE, Fischer. Shell globular and ventricose; aperture oval and canaliculated; operculum spiral. Genus—*Oocorys*, Fischer; abyssal. FAMILY 50. DOLIIDAE, Adams. Shell ventricose, with short spire and wide aperture; no varices and no operculum; foot very broad with projecting anterior angles; siphon long. Genera—*Dolium*, Lamarck; shell with a short canal; ocular tubercles distinct from the tentacles; mantle not reflected over the shell. *Pyrula*, Lamarck; canal long; spire very short; mantle reflected over the shell; eyes sessile (Fig. 71). FAMILY 51. SOLARIIDAE,

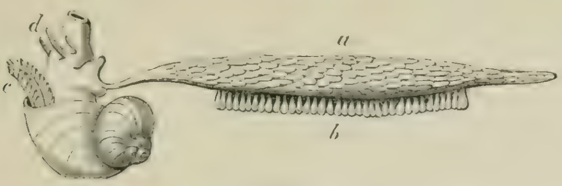

FIG. 135.

Female *Janthina*, with egg-float (*a*) attached to the foot. *b*, egg-capsules; *c*, ctenidium; *d*, cephalic tentacles. (From Lankester, after Owen.)

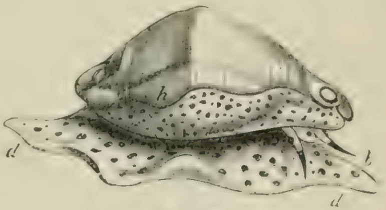

FIG. 136.

Ovula, animal and shell, right-side view. *b*, cephalic tentacles; *d*, foot; *h*, mantle-skirt, which is naturally carried in a reflected condition so as to cover in the sides of the shell. (From Lankester, after Owen.)

Chenu. Shell spiral, conical, with flattened spire, umbilicated; head short; tentacles split throughout their length; foot short. Genera—*Solarium*, Lamarck. *Torinia*, Gray. *Fluxina*, Dall. Family 52. Scalariidae, Broderip. Shell turriculated with numerous whorls and an elongated spire; head short, with a short proboscis; foot small, truncated anteriorly; siphon rudimentary. Genera—*Scalaria*, Lamarck; shell elongate with a circular aperture, whorls very convex, ornamented with longitudinal projecting lamellae; British. *Eglisia*, Gray. *Crossea*, Adams. *Aclis*, Loven.

The three following families of Taenioglossa Platypoda have neither radula nor jaws, and are therefore called Aglossa. They are suctorial animals with a well-developed proboscis, and are often commensal or parasitic on Echinoderms; some are abyssal. The series affords a remarkable example of the regressive evolution of various organs as a result of parasitism. Family 53. Pyramidellidae, Gray. Summit of spire heterostrophic (Fig. 65, B); tentacles deeply grooved externally or split at their extremities; foot truncated anteriorly; a projection, the "mentum," between the head and foot; an operculum present.

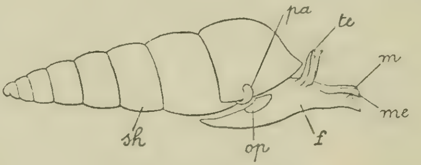

Fig. 137.

Turbonilla scalaris, right-side view. *f*, foot; *m*, mouth; *me*, mentum; *op*, operculum; *pa*, mantle; *sh*, shell; *te*, tentacle. (After Lovén.)

Genera—*Pyramidella*, Lamarck; columella folded, tentacles corniform. *Turbonilla*, Leach; columella not folded (Fig. 137). *Odostomia*, Fleming; columella provided with a tooth; hermaphrodite; British. *Myxa*, Hedley. Family 54. Eulimidae, Adams. Visceral mass still coiled spirally; shell thin and shining, generally with a pointed summit; tentacles without a groove. Genera—*Eulima*, Risso; foot well developed, and with an operculum; animal usually free, but some live in the digestive canal of Holothuriae in the Fiji Islands, in the Philippines, and in Europe, *e.g.* *Eulima distorta* in *Holothuria intestinalis*. *Niso*, Risso. *Scalenostoma*, Deshayes. *Hoplopteron*, Fischer. *Mucronalia*, Adams (=*Stylina*, Fleming); foot reduced, but still operculate; eyes present; animal fixed by its very long proboscis, which is deeply buried in the tissues of an Echinoderm; no pseudopallium. *Stylifer*, Broderip; the operculum is lost, but a rudiment of the foot remains; tentacles very small or absent; eyes, otocysts, and a branchia present; animal fixed by a large proboscis forming a pseudopallium which surrounds the whole of the shell except the more or less projecting extremity of the spire (Fig. 20); sexes separate; parasitic on all groups of Echinoderms in different seas. *Entosiphon*, Koehler and Vaney; visceral mass still coiled; shell much reduced; proboscis very long, forming a pseudopallium, which covers the whole body and projects beyond in the form of a siphon, and serves to put the animal in communication with the external world and for the passage of the ova (Fig. 21); a foot is retained, and also a nervous system and otocysts; neither eyes, branchia, anus, nor rectum; the stomach is a sac with ramifying caeca; hermaphrodite; parasitic in the Holothurian *Deima blakei*, in the Indian Ocean. *Entosiphon* forms the transition to the next family. FAMILY 55. ENTOCONCHIDAE, Fischer (= Cochlosyringia, Voigt). Neither shell nor spirally coiled visceral mass; no sensory organs, nervous system, branchia, or anus; body reduced to a more or less tubular sac; endoparasitic in Holothurians; probably all hermaphrodite, with separate male and female gonads; incubatory ("viviparous"); with conchiferous and operculiferous veliger larvae, without a retractor veli muscle. Genera — *Entocolax*, Voigt; visceral mass essentially genital and forming a swelling surrounded by the pseudopallium; digestive orifice or proboscis at the free extremity; orifice of the pseudopallium at the opposite extremity by which the animal is fixed; a second accessory aperture of the pseudopallium serves for the passage of the genital products. Two species parasitic in Holothurians in the Pacific: *E. ludwigi*, in *Myriotrochus rinkii* from the Behring Sea (Fig. 138); and *E. schiemenzi* in *Chirodota pisanii* from Chili. *Entoconcha*, J. Müller Fig. 139 ; body elongated and tubular; the aperture of the digestive tract rudimentary and situated at the fixed extremity of the body; protandric

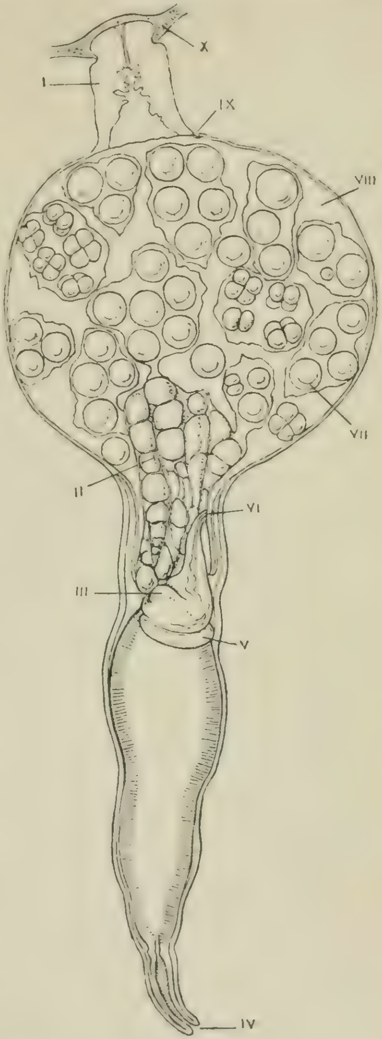

FIG. 138.

Entocolax ludwigi, in situ, × 30. I, fixative apparatus; II, ovary; III, uterus; IV, buccal orifice; V, oviduct; VI, genital orifice; VII, ova separated from the ovary, by dehiscence; VIII, cavity around the ovary, formed by the pseudopallium; IX, orifice of this cavity; X, integument of the Holothuria. (After Voigt.)

hermophrodite with separate male and female gonads; parasitic in the testis of Holothurians, causing their abortion. Three species are known: one in *Synapta digitata* (Mediterranean), one in *Holothuria edulis* (Philippines), and one in a Holothuria from Puget Sound in the North-East Pacific. *Enteroxenos*, Bonnevie; no pseudopallium and no alimentary tract; male and female gonads separate, with a single common genital orifice; larvae operculiferous. *E. ostergreni* (Fig. 140); parasitic in the intestine of *Stichopus* (Norway).

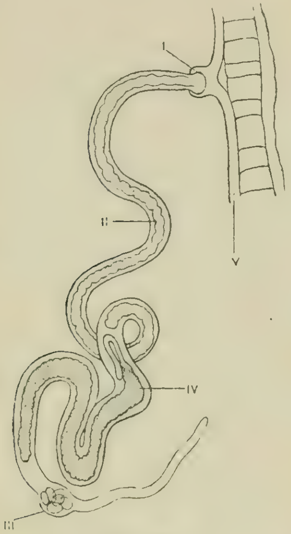

Fig. 139.

Entoconcha mirabilis, in situ, magnified. I, oral extremity; II, remains of the digestive tract; III, testis; IV, ovary; V, antimesenteric vessel of the *Synapta* in which *Entoconcha* is parasite. (After J. Müller.)

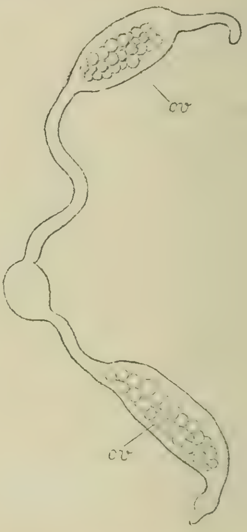

Fig. 140.

Enteroxenos ostergreni, Bonnevie. *ov*, eggs. (After Bonnevie.)

Tribe 2. Heteropoda.

These are free-swimming Taenioglossa, with the foot flattened laterally and the otocysts situated near the cerebral ganglia. There are no mandibles and the intestine is short. All the Heteropoda are pelagic, and are much modified in adaptation to this mode of existence. The foot is very large, and has the form of a fin compressed bilaterally; it bears, in the male at least, a sucker on its ventral aspect (Fig. 142, *d′*). The visceral sac or "nucleus" and mantle form a progressively smaller and smaller part of the mass of the body (compare Figs. 142 and 143), but the head always remains large and forms a cylindrical snout. The cerebral nerve-centres are in juxtaposition; the pleural ganglia, still visible in the Atlantidae and Pterotracheidae, are attached to them, and there are thus two pedal connectives on either side, namely, the cerebro-pedal and the pleuro-pedal; these are separate proximally in *Atlanta*, but fused together for their whole length in other forms. The pedal centres are situated at the base of the fin (Fig. 142, *r*). The visceral commissure is fairly long, is crossed, and bears several ganglia, but there is neither dialyneury nor zygoneury. In the Carinariidae, however, there are secondary uncrossed viscero-pedal anastomoses, and in the Pterotracheidae the pedal connectives are fused with the anterior part of the visceral commissure, and behind the pedal ganglia the two branches of this commissure are fused together for the greater part of their length. The osphradium is a more or less elongated ciliated organ, situated in the pallial cavity to the left of the branchia. The otocysts are situated near the cerebral ganglia (Fig. 141, *u*). The eyes are very large and highly differentiated in structure; they are placed at the sides of the cerebral ganglia and at the bases of the tentacles (Fig. 141, *c*) when the latter organs exist (*Pterotrachea* and the female in some *Firoloida* are devoid of tentacles). The alimentary canal is furnished with a protractile pharynx containing a characteristic Taenioglossate radula with very powerful lateral and marginal teeth. The oesophagus is very long and slightly dilated in the middle of its length. The stomach and liver are situated posteriorly (Fig. 142, *n*), the intestine is always very short, and in the Pterotracheidae it is no longer bent forward (Fig. 143). The heart is situated near the stomach, and in the less specialised Heteropoda (Atlantidae, Carinariidae) is clearly disposed in the same manner as in other Streptoneura, but in the Pterotracheidae, which have undergone detorsion, it has clearly become an opisthobranch

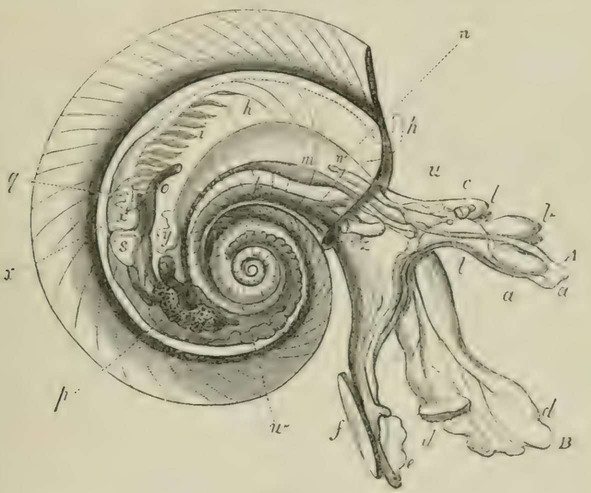

FIG. 141.

Oxygyrus keraudreni, male, right-side view. *A*, head; *a*, mouth and odontophore; *B*, anterior part of the foot; *b*, cephalic tentacles; *c*, eye; *d*, natatory foot and its sucker; *e*, posterior lobe of the foot; *f*, operculum; *h*, mantle and pallial cavity; *i*, ctenidium; *k*, retractor muscle of the foot (columellar muscle); *l*, optic tubercle; *m*, oesophagus; *n*, salivary gland; *o*, rectum and anus; *p*, liver; *q*, kidney; *s*, ventricle; *u*, the otocyst attached to the cerebro-pleural ganglion; *w*, testis; *x*, auricle of the heart; *y*, vesicula seminalis; *z*, penis. (From Lankester, after Souleyet.)

heart. In the Atlantidae there is an aortic bulb ; the arterial vessels always end abruptly in sinuses. The ctenidium is monopectinate and completely enclosed in the pallial cavity in *Atlanta* (Fig. 141, *i*), but it projects in *Carinaria* (Fig. 142, *i*), is no longer covered by the mantle in *Pterotrachea* (Fig. 143, *br*), and finally has completely disappeared in *Firoloida*. The kidney is a transparent and sometimes contractile sac, which has the same relations as in other Taenioglossa and opens not far from the anus (Fig. 141, *q*). The gonad is situated beside the liver (Fig. 141, *w*). The genital duct is always rather short, and opens alongside of the anus ; in the male it exhibits a dilatation, the vesicula seminalis (Figs. 141 and 142, *y*), and its aperture communicates with the penis by means of a seminal groove. The penis is situated at the base of the foot, and is provided with a glandular appendage or flagellum. In the female the genital duct is furnished with a copulatory bursa and an albuminiparous gland. The Heteropoda lay floating eggs imbedded in a gelatinous matrix ; the larvae are characterised by the velum, which is divided into four or six lobes. All the Heteropoda are pelagic and transparent, and are generally found in dense bands in warm and temperate zones, swimming slowly in a reversed position, that is to say, with the foot uppermost. They are all carnivorous. The tribe includes three families which afford a good example of regressive evolution accompanying a process of detorsion and a return to bilateral symmetry, as in the Opisthobranchs. The specialisation of the group is marked by a progressive reduction, and finally by the disappearance first of the operculum, afterwards of the mantle, and finally of the ctenidium and tentacles. The genus *Atlanta* is still provided with a well-developed coiled shell and an operculum, and is

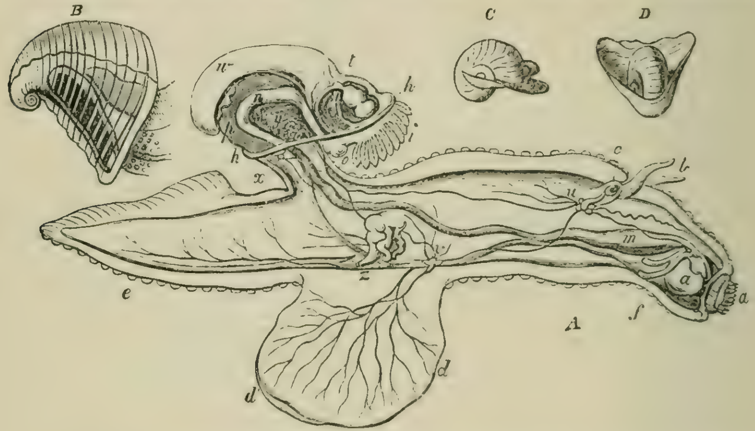

FIG. 142.

Carinaria mediterranea, male, right-side view. *A*, the animal ; *B*, the shell removed ; *C*, *D*, two views of the shell of *Cardiopoda*. *a*, mouth and odontophore ; *b*, cephalic tentacles ; *c*, eye ; *d*, the fin-like anterior lobe of the foot ; *d'*, its sucker ; *e*, posterior part of the foot ; *f*, salivary glands ; *h*, margin of the mantle ; *i*, ctenidium ; *m*, oesophagus ; *n*, stomach ; *o*, anus ; *p*, liver ; *t*, aorta, springing from the ventricle ; *u*, cerebro-pleural ganglion ; *v*, pedal ganglion ; *w*, testis ; *x*, visceral ganglion ; *y*, vesicula seminalis ; *z*, penis. (From Lankester, after Souleyet.)

characteristically prosobranchiate. In *Carinaria* the shell is uncoiled and rudimentary, and there is no operculum. *Pterotrachea* has neither shell nor tentacles and is opisthobranchiate. Finally, *Firoloida* has lost the ctenidium.

FAMILY 1. ATLANTIDAE, Rang. Visceral sac and shell spirally coiled in one plane; foot divided transversely into two parts, the posterior part bearing an operculum with a sinistral coil (Fig. 48), while the anterior part forms a fin provided with a sucker. Genera—*Oxygyrus*, Benson; shell capable of containing the entire animal, carinated only on the last whorl and near the aperture. *Atlanta*, Lesueur; shell capable of containing the whole animal, carinated throughout; aperture with fissures (Fig. 141). FAMILY 2. CARINARIIDAE, Grasset. Visceral sac and shell conical and small in proportion to the rest of the body, which cannot be withdrawn into the shell; foot elongated, fin-shaped, with a sucker but without an operculum. Genera—*Carinaria*, Lamarck (Fig. 142). *Cardiopoda*, d'Orbigny (Fig. 142, C, D). FAMILY 3. PTEROTRACHEIDAE, Gray. Visceral sac very much reduced, without shell and mantle; anus on the posterior part of the body; foot provided with a sucker in the male only. Genera—*Pterotrachea*, Forskål; no tentacles; a ctenidium present; a filiform appendage at the posterior extremity of the foot (Fig. 143). *Firoloida*, Lesueur; tentacles present, but no ctenidium and no posterior appendage to the foot. *Pterosoma*, Lesson.

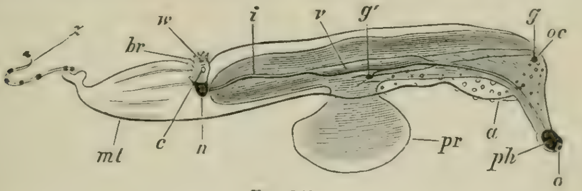

FIG. 143.

Pterotrachea mutica, seen from the right side. *a*, pouch for the reception of the snout when retracted; *br*, ctenidium; *c*, pericardium; *g*, cerebral ganglion; *g′*, pedal ganglion; *i*, intestine; *ml*, posterior part of the foot; *n*, so-called visceral nucleus; *oc*, cephalic eye; *ph*, pharynx; *pr*, fin-like anterior part of the foot; *v*, oesophagus; *w*, osphradium; *z*, caudal appendage. (From Lankester, after Keferstein.)

SUB-ORDER 2. STENOGLOSSA.

Pectinibranchs in which the nervous system is much concentrated and always zygoneurous. The perioesophageal nerve-collar is always posterior to and is not traversed by the salivary glands. The stomatogastric ganglia are situated close to the cerebral nerve-centres and far behind the buccal mass, the last-named organ being greatly reduced. A well-developed proboscis, an unpaired oesophageal gland (the gland of Leiblein or poison-gland), a pallial siphon, and a penis are always present. The osphradium is bipectinate. The radula is narrow, and in the majority of genera (Rachiglossa) has a single lateral on each side of the median or rachidian tooth: in the remainder of the group (Toxiglossa) there is no median tooth, and the radular formula is therefore 1.0.1. The sub-order is accordingly divided into two tribes.

Tribe 1. Rachiglossa.

These are Stenoglossa with a highly-developed proboscis, a pallial siphon, and rudimentary jaws : the radular formula is 1.1.1 (Fig. 74, H).

Family 1. Turbinellidae, Sowerby. Shell solid, piriform, with a thick folded columella ; foot broad ; proboscis long ; tentacles convergent ; lateral teeth of the radula bicuspidate. Genera—*Turbinella*, Lamarck ; shell with short spire and long canal. *Cynodonta*, Schumacher ; spire and canal short ; shell tuberculated. *Fulgur*, Montfort ; shell piriform ; tentacles short. *Hemifusus*, Swainson ; shell fusiform with carinated whorls ; tentacles short (Fig. 99). *Tudicla*, Link. *Strepsidura*, Swainson. Family 2. Fasciolariidae, Adams. Shell elongated, with a long siphon ; head small and narrow, with short tenacles ; foot rather broad and short ; lateral teeth of the radula multicuspidate. Genera—*Fasciolaria*, Lamarck. *Fusus*, Lamarck. *Clavella*, Swainson. *Latirus*, Montfort. Family 3. Mitridae, Adams. Shell fusiform and solid, the spire pointed, the aperture elongated and the columella folded ; no operculum ; tentacles elongated, bearing the eyes at their sides ; foot narrow ; proboscis very long ; siphon moderately long. Genera—*Mitra*, Lamarck. *Turricula*, Klein. *Cylindromitra*, Fischer. *Imbricaria*, Schumacher. Family 4. Buccinidae, Fleming. Foot large and broad ; eyes at the bases of the tenacles ; shell ovoid, with oval aperture ; a horny operculum. Genera—*Chrysodomus*, Swainson ; shell fusiform, solid, with an unguiculate operculum ; British. *Liomesus*, Stimpson ; shell ovoid, with a very short canal ; tentacles short ; lateral teeth of the radula unicuspidate. *Buccinum*, Linnaeus ; shell ventricose with a wide aperture ; operculum oval with sub-central nucleus ; tentacles moderately long ; lateral teeth with three or four cusps ; British. *Cominella*, Gray ; shell fusiform ; the operculum oval to piriform, with an apical nucleus. *Tritonidea*, Swainson ; shell ventricose ; operculum like that of *Cominella*. *Pisania*, Bivona ; shell with a short canal ; operculum unguiculate ; lateral teeth tricuspidate. *Euthria*, Gray ; shell fusiform, with elongate spire and canal. *Phos*, Montfort ; foot broad with two lateral projections anteriorly and a slender posterior filament. *Dipsacus*, Klein ; foot elongated ; tentacles long ; shell ovoid, solid, with a short canal ; lateral teeth bicuspidate. Family 5. Nassidae, Swainson. Foot broad, with two slender posterior appendages ; siphon long ; shell ovoid, with a short canal ; operculum unguiculate. Genera — *Nassa*, Lamarck ; external border of the aperture of the shell thickened ; marine ; British. *Canidia*, Adams ; exterior border of the aperture simple ; fluviatile. *Bullia*, Gray ; shell polished ; tentacles without eyes ; foot very broad ; a burrowing form. Family 6. Muricidae, Fleming. Foot truncated anteriorly ; tentacles elongated, bearing the eyes on their sides, more or less high up ; shell with moderately long spire and canal, ornamented with ribs, often spiny. Genera—*Murex*, Linnaeus ; eyes half-way up the tentacles ; canal almost closed ; British. *Trophon*, Montfort ; eyes at the bases of the tentacles ; shell lamellar ; canal open ; British. *Typhis*, Montfort ; shell with closed canal and tubular spines. *Urosalpinx*, Stimpson. *Lachesis*, Risso. Family 7. Purpuridae, Broderip. Foot short, obtuse posteriorly ; shell thick with a short spire, the last whorl large and the canal short ; aperture wide ; columella flattened ; operculum horny. Genera—*Purpura*, Bruguière ; shell not umbilicated, aperture smooth ; British. *Rapana*, Schumacher ; shell ventricose, umbilicated. *Monoceros*, Lamarck ; shell like that of *Purpura*, but the aperture shifted backward and bearing a conical tooth on its external border. *Sistrum*, Montfort ; shell thick, spiny, the aperture contracted by the thickening of the margins of the aperture. *Concholepas*, Lamarck ; shell ovoid, the spire short and the aperture widely dilated. Family 8. Haliidae, Fischer. Foot large and thick ; without an operculum ; tentacles thick and flattened ; shell ventricose, thin, and smooth, with a wide aperture. Genus—*Halia*, Risso ; from Cadiz and Morocco. Family 9. Cancellariidae, Adams. Snout short ; tentacles long, with the eyes at their bases and external ; foot small ; no operculum ; siphon short ; shell ovoid with short spire and folded columella. Genus — *Cancellaria*, Lamarck. Family 10. Columbellidae, Adams. Foot large, tentacles long and convergent ; spire of shell prominent, aperture narrow, the canal very short and the columella crenelated. Genus — *Columbella*, Lamarck. Family 11. Coralliophilidae, Chenu. Foot short ; tentacles slender and convergent ; siphon short ; radula absent ; shell irregular ; sedentary animals living in corals. Genera—*Coralliophila*, Adams ; shell deformed, with a wide aperture and a short canal ; operculum present. *Rhizochilus*, Steenstrup ; no operculum ; the aperture of the shell irregular, with the canal prolonged into a tube. *Leptoconchus*, Rüppel ; no operculum ; the shell globular with a wide aperture. *Magilus*, Montfort ; an operculum present ; the last whorl of the shell uncoiled and very thick. *Rapa*, Klein ; an operculum present ; shell globular and umbilicated, the aperture provided with a canal. Family 12. Volutidae, Gray. Head very flattened, and transversally widened, with the eyes on the sides ; snout short ; foot broad ; siphon with internal appendages. Genera — *Voluta*, Linnaeus ; head with eyes ; Australian seas. *Guivillea*, Watson ; no eyes ; abyssal. *Cymba*, Broderip and Sowerby ; viviparous. Family 13. Olividae, d'Orbigny. Eyes, when present, on the middle of the tentacles ; fore part of the foot with a transverse groove ; a posterior pallial tentacle ; generally burrowing. Genera—*Oliva*, Bruguière ; eyes ; no operculum. *Olivella*, Swainson ; tentacles without eyes ; an operculum. *Ancillaria*, Lamarck. *Agaronia*, Gray. Family 14. Marginellidae, Adams. Foot very large ; mantle reflected over the shell. Genera—*Marginella*, Lamarck ; foot without operculum ; a central gland-pore. *Pseudomarginella*, Carrière ; foot with an operculum and an anterior gland-

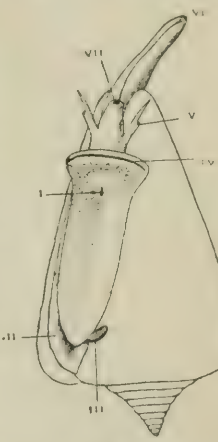

Fig. 144.

Conus lineatus, ventral aspect. I, orifice of the pedal gland ; II, mantle and opening of the pallial cavity ; III, operculum ; IV, anterior glandular groove of the foot ; V, eye and tentacle ; VI, siphon ; VII, mouth. (After Souleyet.)

pore. Family 15. Harpidae, Chenu. Foot very great; without operculum; shell with a short spire and longitudinal ribs; siphon long. Genus—*Harpa*, Lamarck.

Tribe 2. Toxiglossa.

Stenoglossa without jaws, and with a radular formula of 1.0.1; a "poison gland" present, whose duct traverses the nerve-collar.

Family 1. Pleurotomatidae, Loven. Shell fusiform with an elongated spire; the margin of the shell and mantle notched; siphon rather long; eyes situated on the sides of the tentacles. Genera—*Clavatula*, Lamarck; operculum piriform with a lateral nucleus; eyes near the extremities of the tentacles. *Pleurotoma*, Lamarck; operculum oval with nucleus near the summit; eyes near the bases of the tentacles. *Mangilia*, Risso; no operculum; eyes half-way up the tentacles. *Bela*, Gray. *Pusionella*, Gray. *Pontiothauma*, Smith. Family 2. Terebridae, Adams. Shell turriculated, with numerous whorls; aperture and operculum oval; foot small; eyes at the summits of the tentacles; siphon long. Genus—*Terebra*, Adanson. Family 3. Conidae, Gray. Shell conical, with a very short spire and a narrow aperture with parallel borders; eyes borne near the middle of the external sides of the tentacles; an unguiform operculum. Genus—*Conus*, Linnaeus (Fig. 144).

Sub-Class II. Euthyneura, Spengel
(=Platymalakia, von Jhering=Androgyna, Mörch).

These are hermaphrodite Gastropoda, whose radula is generally composed of uniform teeth on each side of the median tooth (Fig. 145). The head in most cases bears two pairs of tentacles; it is only in *Lophocercus*, the Elysiomorpha, *Hedyle milaschewitchi*, and the Janellidae that there is a single pair. The Euthyneura are specially characterised by the detorsion of their organisation when adult; this detorsion is particularly well manifested in the visceral commissure, which is no longer twisted, except in some archaic forms of Tectibranchs (*Actaeon*, Fig. 57) and Pulmonates (*Chilina*), and shows a tendency to the concentration of all its elements round the oesophagus (Fig. 146). To such a degree is this concentration carried that, with the exception of the majority of the Bullomorpha and of *Aplysia* (Fig. 95), the whole central nervous system is aggregated in the cephalic region (Fig. 97), sometimes on the dorsal side, as in the Pleurobranchidae and Nudibranchia (Fig. 159), sometimes on the ventral side as in the Thecosomata (Fig. 60, *n.s*). The pedal centres are frequently united by a second "parapedal"

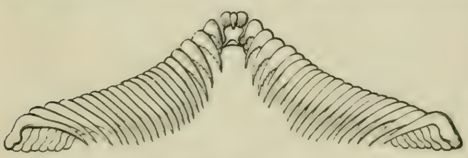

Fig. 145.

Acera bullata, a single row of teeth of the radula; formula: $\infty.1.\infty$. (From Lankester, after Loven.)

(Figs. 95, *pe*, and 96, *g.pe*) commissure. The sub-class includes the two orders, Opisthobranchia and Pulmonata.

ORDER 1. **Opisthobranchia**, Milne-Edwards.

Marine Euthyneura with aquatic respiration; the ventricle of the heart is generally anterior, and the pallial cavity, when present, is widely open. There is a marked tendency to a reduction of the shell, which may become internal or disappear. In the naked forms spicules are sometimes developed (Pleurobranchidae, Doridomorpha, Hedylidae, Fig. 168, *sp.*). The order comprises two suborders, Tectibranchia and Nudibranchia.

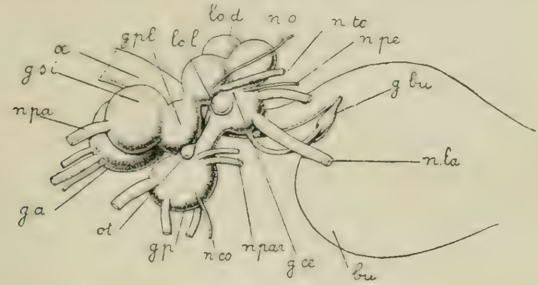

FIG. 146.

Central nervous system of *Limnaea stagnalis*, right-side view. *bu*, buccal mass; *g.a*, abdominal ganglion; *g.bu*, buccal or stomato-gastric ganglion; *g.ce*, cerebral ganglion; *g.p*, pedal ganglion; *g.pl*, pleural ganglion; *g.s.i*, supra-intestinal ganglion; *lo.d*, dorsal lobe of cerebral ganglion; *lo.l*, lateral lobe of cerebral ganglion; *n.co*, columellar nerve; *n.la*, labial nerve; *n.o.* optic nerve; *n.pa*, right pallial nerve; *n.par*, parietal nerves; *n.pe*, penial nerve; *n.te*, tentacular nerve; *oe*, oesophagus; *ot*, otocyst and nerve.

SUB-ORDER 1. TECTIBRANCHIA, Cuvier.

Opisthobranchs provided in the adult state with a mantle and a shell, with the exceptions *Runcina*, *Pleurobranchaea*, the Cymbuliidae, and some Aplysiomorpha. There is a ctenidium, except in some "Thecosomata" and "Gymnosomata," and an osphradium. The sub-order includes three tribes, the Bullomorpha, the Aplysiomorpha, and the Pleurobranchomorpha.

TRIBE 1. BULLOMORPHA.

In these Tectibranchs the shell is usually well developed (it is wanting in *Runcina* and the Cymbuliidae), and may be external or internal. There is no operculum except in the Actaeonidae and Limacinidae (Fig. 49, *op*). The pallial cavity is always well developed, and contains the ctenidium, in part at least: this ctenidium, except in the Lophocercidae, is of the "folded" type. With the exception of the Aplustridae, Lophocercidae, and Thecosomata, the head is devoid of apparent tentacles, and its dorsal surface forms a digging disc or shield usually separate from the neck, and with more or less scolloped margins. The edges of the foot (parapodia) are continuous with the ventral face of that organ (Fig. 147, *f*), and are often transformed into highly-developed fins (Fig. 151, VI).

Posteriorly the mantle forms a large "pallial lobe" under the pallial aperture (Figs. 98, *i.l*; 148, I). The stomach is generally provided with chitinous, or even calcified, masticatory plates (Fig. 76, *m.p*). The visceral commissure is fairly long, except in such specialised forms as *Runcina*, *Lobiger*, and the Thecosomata (Fig. 60, *n.s*). The hermaphrodite genital aperture is connected with the penis by a ciliated groove, except in *Actaeon* (Fig. 148), *Lobiger*, and *Cavolinia longirostris*, in which the spermiduct is a closed tube. The Bullomorpha are swimmers or burrowers.

Family 1. Actaeonidae, Adams. Cephalic shield bifid posteriorly; the margins of the foot slightly developed; the genital ducts diaulic; the visceral commissure streptoneurous; the shell thick, with a prominent spire and elongated aperture; columella generally folded; a corneous paucispiral operculum. Genera—*Actaeon*, Montfort; British (Fig. 148). *Solidula*, Fischer von Waldheim. *Tornatellæa*, Conrad; extinct. *Triploca*, Tate; from the Eocene. *Adelactaeon*, Cossmann. *Actaeonina*, d'Orbigny; Carboniferous to recent. *Bullina*, Férussac. *Bullinula*, Beck. *Actaeonella*, d'Orbigny; from the Cretaceous. *Volvaria*, Lamarck; Eocene. *Odostomiopsis*, Thiele. Family 2. Ringiculidae, Fischer. Cephalic disc enlarged anteriorly and forming an open tube posteriorly; shell external, thick, with a prominent spire; no operculum. Genera—*Ringicula*, Deshayes. *Pugnus*, Hedley. *Cinulia*, Gray; from the Cretaceous. *Avellana*, d'Orbigny; from the Cretaceous. *Fortisia*, Bayan; from the Eocene. Family 3. Tornatinidae, Fischer. Margins of the foot not prominent; no radula; shell external with inconspicuous spire; no operculum. Genera—*Tornatina*, Adams; British. *Retusa*, Brown. *Volvula*, Adams. Family 4. Scaphandridae, Fischer. Cephalic shield short, truncated posteriorly; eyes deeply imbedded; three calcareous stomachal plates, two broad and paired, one narrow and azygos; shell external, with reduced spire. Genera—*Scaphander*, Montfort; British. *Sabatia*, Bellardi; Eocene. *Atys*, Montfort. *Smaragdinella*, Adams. *Cylichna*, Loven; British. *Amphisphyra*, Loven; British. Family 5. Bullidae, d'Orbigny. Margins of the foot well developed; eyes superficial; three chitinous stomachal plates; shell external, with reduced

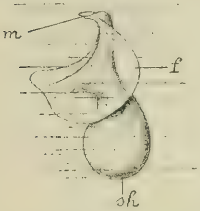

Fig. 147.

Acera bullata, swimming, left-side view. *f*, fin (foot); *m*, mouth; *sh*, shell. (After Guiart.)

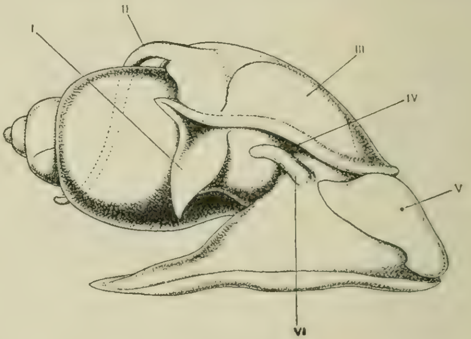

Fig. 148.

Actaeon tornatilis, removed from its shell, right-side view. I, inferior lobe of the mantle; II, glandular hollow pallial appendage (extending to the first whorls); III, pallial (hypobranchial) gland; IV, opening of the pallial cavity; V, eye and cephalic hood; VI, penis.

spire. Genera—*Bulla*, Linnaeus; British. *Haminea*, Leach; British (Fig. 98). Family 6. Aceratidae, Pilsbry. Cephalic shield continuous with the neck; twelve to fourteen chitinous stomachal plates; a posterior pallial filament passing through a notch in the shell. Genera—*Acera*, O. F. Müller; British (Fig. 147). *Cylindrobulla*, Fischer. *Volvatella*, Pease. Family 7. Aplustridae, Chenu. Foot very broad; cephalic shield with four tentacles; shell external, thin, without prominent spire. Genera—*Hydatina*, Schumacher (Fig. 149). *Aplustrum*, Schumacher. *Micromelo*, Pilsbry. Family 8. Philinidae, Adams. Cephalic shield broad, thick, and simple; shell wholly internal, thin, the spiral much reduced and the aperture very large. Genera—*Philine*, Ascanius (Fig. 58); gizzard with three similar calcareous masticatory plates; British. *Cryptophthalmus*, Ehrenberg. *Chelinodura*, Adams. *Phanerophthalmus*, Adams. *Colpodaspis*, Sars; British. *Colobocephalus*, Sars. Family 9. Doridiidae, Fischer. Cephalic shield ending posteriorly in a median point; mantle well developed; shell internal, largely membranous; digestive canal without radula and without masticatory plates. Genera — *Doridium*, Meckel. *Navarchus*, Cooper. Family 10. Gastropteridae, Fischer. Cephalic shield pointed behind; shell internal, chiefly membranous with a calcified nucleus, nautiloid; parapodia well developed, forming fins. *Gastropteron*, Kosse. Family 11. Runcinidae, Adams. Cephalic shield continuous with the dorsal integuments of the body; no shell; ctenidium projecting from the mantle cavity; four stomachal plates. Genus—*Runcina*, Forbes; British. Family 12. Lophocercidae, Adams. Shell globular or ovoid, external; foot elongated, the parapodia separate from the ventral surface of the foot; genital duct diaulic; visceral commissure short. Genera—*Lobiger*, Krohn; parapodia divided into two fins on each

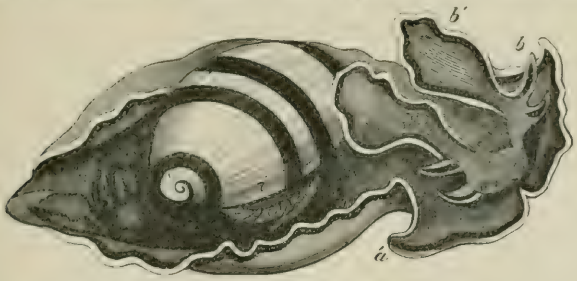

Fig. 149.

Hydatina vexillum, as seen crawling. *a′*, anterior part of the foot; *b*, *b′*, cephalic tentacles; *i*, shell. (From Lankester, after Adams.)

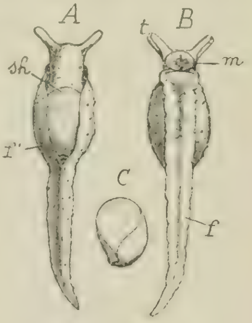

Fig. 150.

Lophocercus sieboldi. *A*, dorsal aspect; *B*, ventral aspect; *C*, the shell. *f*, foot; *f′*, parapodia or anterior lateral lobe of foot, reflected on the shell; *m*, mouth; *sh*, shell; *t*, tentacle. (After Souleyet.)

side; two pairs of tentacles; Mediterranean. *Lophocercus*, Krohn; parapodia undivided and applied to the shell; a single pair of tentacles; Mediterranean (Fig. 150). Family 13. Limacinidae, Gray. Dextral animals with visceral mass and shell coiled "pseudo-sinistrally" (ultra-dextrally); operculum with sinistral spiral; pallial cavity dorsal. Genera—*Peraclis*, Forbes; head proboscidiform, with symmetrical tentacles; a ctenidium. *Limacina*, Cuvier; head much reduced; the right tentacle larger than the left (Fig. 63); British. Family 14. Cymbuliidae, Cantraine. Adult without shell; a sub-epithelial pseudoconch formed by the connective tissue; pallial aperture ventral. Genera—*Cymbulia*, Péron and Lesueur; pseudoconch thick; foot with a median ventral filament (Fig. 151). *Cymbuliopsis*, Pelseneer; pseudoconch thin, with a large cavity. *Gleba*, Forskål; pseudoconch thin, with scarcely any cavity. *Desmopterus*, Chun; each fin with a posterior filament. Family 15. Cavoliniidae, d'Orbigny. Visceral mass and shell not coiled, symmetrical; pallial aperture ventral. Genera—*Cavolinia*, Abildgaard; visceral mass and shell more or less flattened dorso-ventrally (Fig. 153); pallial appendages present which pass through lateral fissures in the shell. *Clio*, Browne; mantle without projecting appendages; shell not septate; universally distributed (Fig. 152). *Cuvierina*, Boas; shell with a posterior septum; circular in section. The three last families form the group formerly known as "Thecosomatous Pteropods." These animals are characterised, in contrast to other allied Mollusca, by the foot, which is entirely transformed into two anterior symmetrical fins; by the existence of a mantle and mantle-cavity; by the absence of eyes in the adult; by the absence of a ctenidium, except in

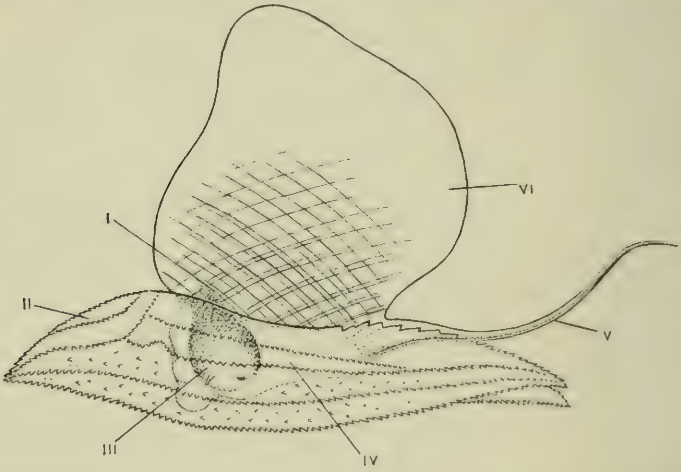

Fig. 151.

Cymbulia peroni, swimming, left-side view. I, position of the mouth, seen through the fin; II, the sub-epithelial pseudoconch; III, visceral mass; IV, pallial cavity; V, posterior flagellum of the foot; VI, left fin. (After Delle Chiaje.)

certain species of *Peraclis* and *Cavolinia*; and by the position of the nerve-centres at the sides and on the ventral side of the oesophagus. All three families are pelagic.

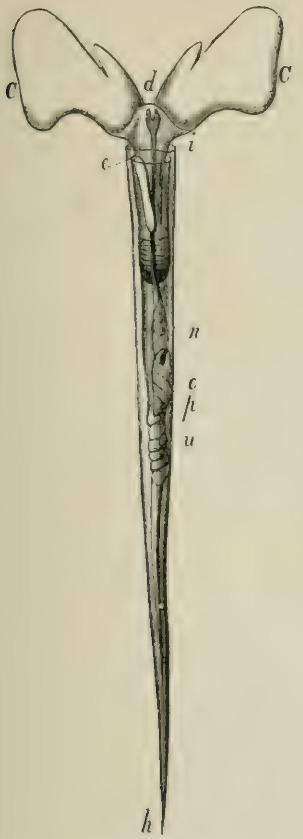

Fig. 152.

Clio acicula, ventral aspect. *C*, wing-like lateral lobe of the foot; *d*, median posterior lobe of the foot; *e*, genital opening; *h*, pointed extremity of the shell; *i*, anterior margin of the shell; *n*, stomach; *o*, liver; *p*, heart; [illegible], hermaphrodite gland. (From Lankester, after Souleyet.)

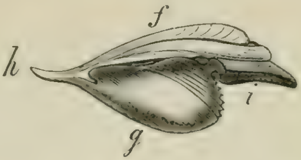

Fig. 153.

Shell of *Cavolinia tridentata*, seen from the right side. *f*, postero-dorsal surface; *g*, antero-ventral surface; *h*, median dorsal spine; *i*, mouth of the shell. (From Lankester, after Souleyet.)

Tribe 2. Aplysiomorpha.

In these Tectibranchs the shell is always much reduced and more or less internal, or it may be altogether lost in the adult, *e.g.* in *Phyllaplysia* and the Gymnosomata. The head bears two pairs of tentacles. The margins of the foot, or parapodia, are separate from the ventral surface and are generally transformed into natatory lobes (Fig. 155, *fi*). The visceral commissure, except in *Aplysia*, is very much shortened. The genital duct is monaulic; the hermaphrodite duct is connected with the penis by a ciliated groove (Fig. 154). The animals comprised in this tribe are crawling or swimming forms.

Family 1. Aplysiidae, d'Orbigny. The shell partly covered in, or internal (absent in *Aplysiella*); the foot long, with well-developed ventral surface. Genera—*Aplysia*, Linnaeus; shell incompletely covered; parapodia broad; visceral commissure long; British (Fig. 154). *Dolabella*, Lamarck. *Dolabrifer*, Gray. *Aplysiella*, Fischer; shell only slightly covered in; parapodia slightly developed; visceral commissure short. *Phyllaplysia*, Fischer; parapodia slightly developed; no shell. *Notarchus*, Cuvier; shell internal, much reduced; parapodia fused together dorsally to form a contractile sac surrounding but not attached to the visceral sac.

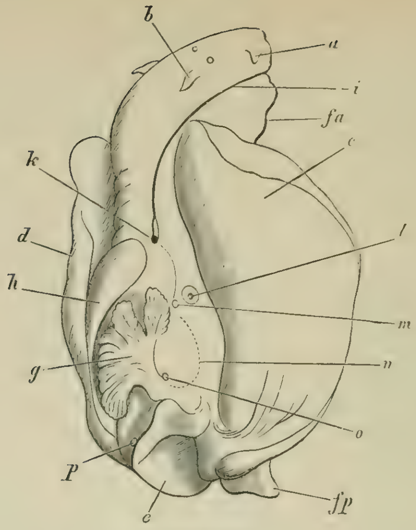

FIG. 154.

Aplysia leporina (dorsal aspect), with the parapodia and mantle reflected from the mid-line. *a*, anterior cephalic tentacle; *b*, posterior tentacle (between *a* and *b*, the eyes); *c*, right parapodia; *d*, left parapodia; *e*, hinder part of visceral hump; *f.a*, anterior part of the foot, underlying the head; *f.p*, posterior extremity of the foot; *g*, ctenidium; *h*, the mantle-skirt tightly spread over the horny shell and pushed with it towards the left side; *i*, the spermatic groove; *k*, the common genital pore; *l*, orifice of the grape-shaped gland; *m*, osphradium; *n*, outline of part of the renal sac below the surface; *o*, external aperture of the kidney; *p*, anus. (After Lankester.)

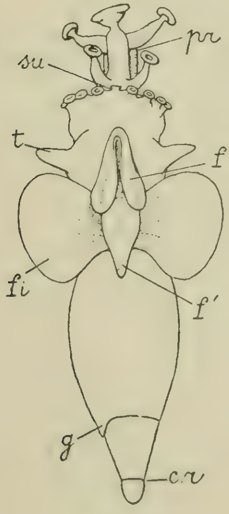

FIG. 155.

Dexiobranchaea paucidens, Boas, ventral aspect, $\frac{14}{1}$. *c.r*, posterior ciliated ring; *f*, anterior part of the foot; *f'*, posterior part of the foot; *fi*, fins or parapodia; *g*, gill; *pr*, proboscis; *su*, suckers; *t*, tentacle. (After Boas.)

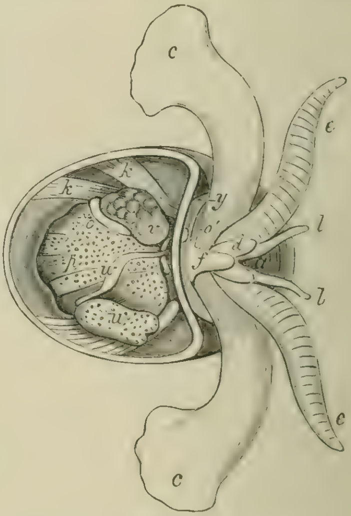

FIG. 156.

Halopsyche gaudichaudi, ventral aspect, the body-wall removed, the head to the right-hand side. *a*, the mouth; *c*, the fin-like lateral lobes of the foot; *d*, the anterior median part of the foot; *e*, cephalic tentacles; *f*, the posterior median part of the foot; *k*, retractor muscles; *l*, appendages of the cephalic tentacles; *o'*, anus; *o*, *p*, liver; *u*, *v*, *w*, genitalia; *y*, genital pore. (From Lankester, after Souleyet.)

FAMILY 2. PNEUMONODERMATIDAE, Gray. Shell and mantle absent; foot shorter than the visceral mass, and with a much-reduced ventral surface; parapodia highly developed and fin-shaped; pharynx evaginable, with suckers. Genera—*Dexiobranchaea*, Boas; suckers independent; no terminal posterior branchia. *Pneumonoderma*, Cuvier; suckers united on two lobes; a quadriradiate terminal branchia. *Spongiobranchaea*, d'Orbigny; a simple annuliform terminal branchia. *Schizobrachium*, Meisenheimer; acetabuliferous appendages ramified. FAMILY 3. CLIONOPSIDAE, Costa. No buccal appendages or suckers; a very long evaginable proboscis; a quadriradiate terminal branchia. Genus—*Clionopsis*, Troschel. FAMILY 4. NOTOBRANCHAEIDAE, Pelseneer. Posterior branchia triradiate. Genus—*Notobranchaea*, Pelseneer. FAMILY 5. THLIPTODONTIDAE, Kwietniewski. Head very large, not marked off from the body; neither branchia nor suckers; fins situated near the middle of the body. Genus—*Thliptodon*, Boas. FAMILY 6. CLIONIDAE, Gray. No branchia of any kind; a short evaginable pharynx, bearing paired conical buccal appendages or "cephalocones." Genera—*Clione*, Pallas. *Paraclione*, Tesch. *Fowlerina*, Pelseneer. FAMILY 7. HALOPSYCHIDAE, Pelseneer. No branchia; two long and branched buccal appendages. Genus—*Halopsyche*, Boas (Fig. 156).

The last six families form the group formerly known as the "Gymnosomatous Pteropoda," characterised by the absence of the mantle and shell, the reduction of the ventral surface of the foot, and the fin-shaped parapodia placed at the anterior end of the body. They are all pelagic.

TRIBE 3. PLEUROBRANCHOMORPHA.

In these Tectibranchs there are two pairs of tentacles. The foot is devoid of parapodia. There is no pallial cavity, but there is always a single ctenidium situated on the right side and occupying the space between the mantle and the foot. The genital duct is diaulic, without an open seminal groove; the male and female apertures are contiguous. The visceral commissure is short, and resembles that of the Nudibranchs in showing a tendency to the fusion of the supra-intestinal and sub-intestinal with the pleural ganglia, and the concentration of all the ganglia on the dorsal side of the oesophagus.

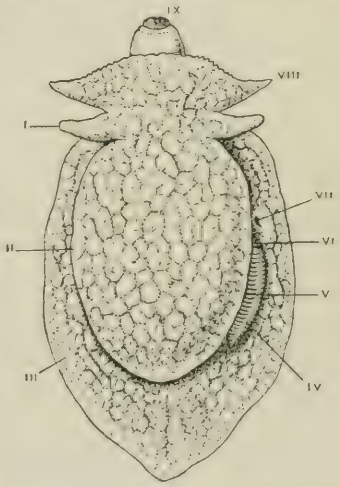

FIG. 157.

Pleurobranchaea meckeli, dorsal aspect. I, posterior tentacle or rhinophore; II, mantle; III, foot; IV, gill; V, position of the anus, under the mantle; VI, orifice of Bourne's prebranchial gland; VII, genital (hermaphrodite) orifice; VIII, the fused anterior tentacles; IX, expanded proboscis.

FAMILY 1. TYLODINIDAE, Mazzarelli. Shell external and conical; the anterior tentacles form a frontal veil; the ctenidium extending only over the right side; a distinct osphradium. Genus—*Tylodina*, Rafinesque;

Mediterranean. FAMILY 2. UMBRELLIDAE, Gray. Shell external, conical, and much flattened; anterior tentacles very small and situated together with the mouth in a notch in the foot below the head; ctenidium very large, extending above the neck. Genus—*Umbrella*, Lamarck (Fig. 158). FAMILY 3. PLEUROBRANCHIDAE, Gray. Shell covered by the mantle or absent; the interior tentacles form a frontal veil; spicules are formed in the mantle; foot flattened. Genera—*Pleurobranchus*, Cuvier; mantle long and broad; shell internal, with a short spire. *Berthella*, Blainville. *Haliotinella*, Souverbie. *Oscanius*, Leach; British. *Oscaniella*, Bergh. *Oscaniopsis*, Bergh. *Pleurobranchaea*, Meckel; mantle short and narrow; no shell (Fig. 157).

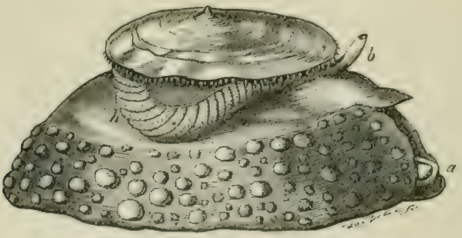

FIG. 158.

Umbrella mediterranea, right side view. *a*, mouth; *b*, cephalic tentacle; *h*, ctenidium. The free edge of the mantle is seen just below the margin of the shell. (From Lankester, after Owen.)

SUB-ORDER 2. NUDIBRANCHIA, Cuvier.

Naked Opisthobranchs without a shell in the adult state; without ctenidium and osphradium. These animals are generally slug-like and exhibit an external symmetry. The visceral mass, except in the Hedylidae, is no longer a sac marked off from the foot, and the dorsal integuments frequently give rise to appendages which are subservient to respiration. The nervous system is much concentrated; the ganglia are generally united on the dorsal side of the oesophagus; the supra-intestinal and infra-intestinal ganglia are fused with the pleurals (Fig. 159, *a*); the fusion of the centres is sometimes carried to a great extent (*Tethys*), but the several infra-oesophageal commissures (pedal, visceral, and stomato-gastric) always remain distinct. The visceral commissure is always reduced, and is generally without a ganglion. Accessory stomato-gastric or "gastro-oesophageal" ganglia are present. The gonad is subdivided into male and female acini (Fig. 102, B) except in the Elysiomorpha. The Nudibranchia are marine, generally carnivorous, and brightly coloured, affording many instances of mimicry. There is no osphradium, but its absence is compensated by the increased development of the olfactory organ or rhinophore. In ontogeny the free veliger stage of Nudibranchs (Fig. 61) is followed by a planariform creeping stage, during which the shell is rapidly lost (Fig. 116, B); and finally the dorsal appendages are acquired, notably the dorsal papillae of the Eolids, of which the most anterior are the first to be developed. *Cenia* is the only form that leaves the egg in the adult condition; it has no embryonic shell, and the embryonic velum is extremely reduced. The phylogenetic relationships between the Nudibranchs and Tectibranchs are clearly exhibited by the organisation of the Pleurobranchomorpha, in which there is neither a pallial cavity nor an osphradium, and the respiration is largely pallial. The shell is altogether absent in *Pleurobranchaea*; the nervous system is concentrated on the dorsal side of the oesophagus; spicules and cnidocysts are found in the dorsal integuments. The mantle of the Doridomorpha is completely homologous with that of the Pleurobranchidae, and is in no wise to be regarded as an epipodium reflected over the dorsal surface of the body.

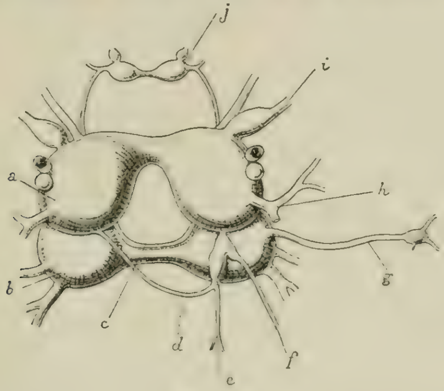

FIG. 159.

Nervous system of *Goniodoris*, dorsal view. *a*, cerebro-pleural ganglion, with eye and otocyst; *b*, pedal ganglion; *c*, sub-cerebral commissure; *d*, visceral commissure; *e*, visceral nerve; *f*, genital nerve; *g*, penial nerve; *h*, pallial nerve; *i*, tentacular nerve and ganglion; *j*, stomatogastric ganglion.

TRIBE 1. TRITONIOMORPHA.

Nudibranchia in which the liver is wholly or partially contained in the visceral mass. The anus is lateral, on the right side. There are generally two rows of ramified dorsal appendages (Fig. 83, II). The genital duct is diaulic; the male and female orifices contiguous. FAMILY 1. TRITONIIDAE, Adams. The anterior tentacles form a frontal veil; the foot rather broad. Genera—*Tritonia*, Cuvier; stomach without horny plates; British (Fig. 83). *Marionia*, Vayssière; stomach with horny plates. FAMILY 2. SCYLLAEIDAE, Alder and Hancock. No anterior tentacles; dorsal appendages broad and foliaceous; foot very narrow; stomach with horny plates. Genus—*Scyllaea*, Linnaeus; pelagic. FAMILY 3. PHYLLIRHOIDAE, Adams. No anterior tentacles and no dorsal appendages; body laterally compressed; transparent natatory forms. Genus—*Phyllirhoë*, Péron and Lesueur (Fig. 161). FAMILY 4. TETHYIDAE, Alder and Hancock. Head broad, surrounded by a funnel-shaped velum or hood; no radula; dorsal appendages foliaceous. Genera—*Tethys*, Linnaeus; foot broad; no mandibles (Fig. 160, B). *Melibe*, Rang; foot narrow; mandibles present. FAMILY 5. DENDRONOTIDAE, Alder and Hancock. Anterior tentacles forming a scolloped frontal veil; dorsal appendages and tentacles similarly ramified. Genera—*Dendronotus*, Alder and Hancock;

British. *Campaspe*, Bergh. FAMILY 6. BORNELLIDAE, Fischer. The dorsum garnished on either side with papillae at the bases of which are ramified appendages. Genus—*Bornella*, Gray. FAMILY 7. LOMANOTIDAE, Bergh. Body flattened; the two dorsal borders prominent and foliaceous Genus—*Lomanotus*, Verany; British.

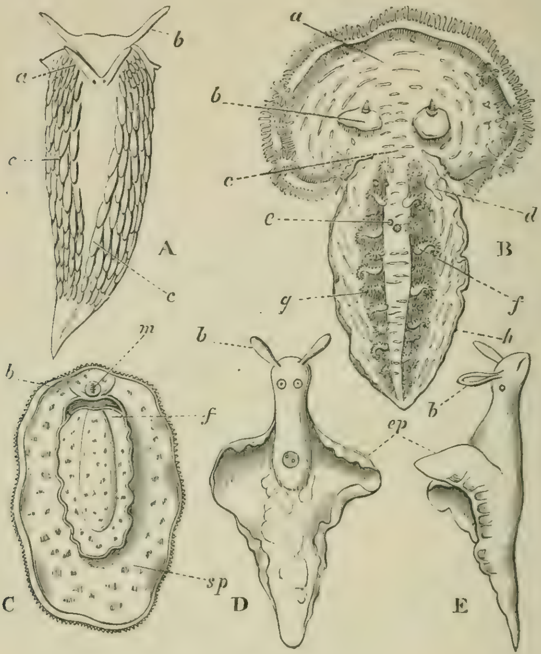

FIG. 160.

A, *Eolis papillosa*, dorsal view; *a*, posterior cephalic tentacle (rhinophore); *b*, anterior cephalic tentacle; *c*, the dorsal papillae. *B*, *Tethys leporina*, dorsal view; *a*, the cephalic hood; *b*, cephalic tentacle; *c*, neck; *d*, genital pore; *e*, anus; *f*, large dorsal papillae; *g*, smaller dorsal papillae; *h*, margin of the foot. *C*, *Doris tuberculata*, seen from the pedal surface; *b*, margin of the head; *f*, sole of the foot; *m*, mouth; *sp*, the mantle. *D*, *E*, dorsal and lateral view of *Elysia viridis*; *b*, tentacle; *ep*, lateral outgrowths. (From Lankester, after Hancock, Cuvier, and Allmann.)

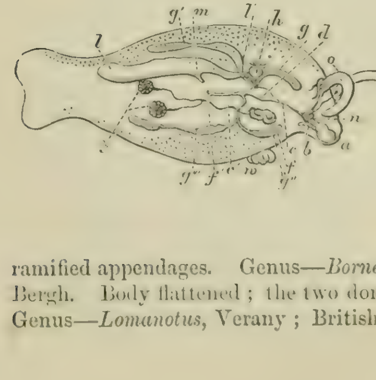

FIG. 161.

Phyllirhoë bucephalum, right-side view; the internal organs are shown as seen by transmitted light. *a*, mouth; *b*, radular sac; *c*, oesophagus; *c'*, intestine; *d*, stomach; *f*, the genital pore; *f'*, anus; *g*, *g'*, *g''*, *g'''*, the four lobes of the liver; *h*, the heart (auricle and ventricle); *l*, the renal sac; *l'*, the ciliated reno-pericardial duct; *m*, the external opening of the renal sac; *n*, the cerebral ganglion; *o*, the cephalic tentacles; *w*, the parasitic medusa *Mnestra*, usually found attached in this position; *y*, the ovo-testes. (From Lankester, after Keferstein.)

TRIBE 2. DORIDOMORPHA.

Nudibranchia with external symmetry, in consequence of the median position of the anus, which is posterior and generally dorsal, and surrounded by ramified pallial appendages constituting a secondary branchia (Fig. 162, *g*). The liver is not ramified in the integuments. The genital duct triaulic. Spicules present in the mantle.

FAMILY 1. POLYCERATIDAE, Abraham. A more or less prominent frontal veil; branchiae non-retractile. Genera—*Euplocamus*, Philippi (Fig. 162); ramified dorsal appendages on the border of the mantle. *Polycera*, Cuvier; the mantle border bears on each side a single posterior pointed appendage; British. *Thecacera*, Johnston; the mantle border with club-shaped appendages; the branchia formed of three lobes directed forwards; British. *Aegirus*, Loven; body tuberculate; rhinophores not lamellar; a dorsal mandible; British. *Plocamophorus*, Leuckart. *Palio*, Gray. *Crimora*, Alder and Hancock. *Triopa*, Johnston, British. *Triopella*, Sars. FAMILY 2. GONIODORIDIDAE, Adams. Mantle border projecting; frontal veil reduced and often covered by the anterior border of the mantle. Genera—*Goniodoris*, Forbes; frontal veil not continuous with the mantle; mantle quadrangular and incised posteriorly; British. *Acanthodoris*, Gray; mantle oval, papillate; rhinophores retractile; British. *Idalia*, Leuckart; mantle reduced and fringed with long appendages;

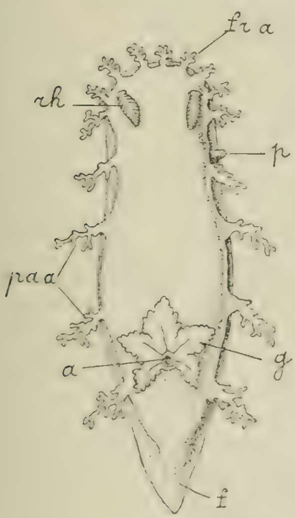

FIG. 162.

Euplocamus croceus, dorsal aspect. *a*, anus; *f*, foot; *fr.a*, frontal appendages; *g*, gill; *pa.a*, pallial appendages; *rh*, rhinophore. (After Vayssière.)

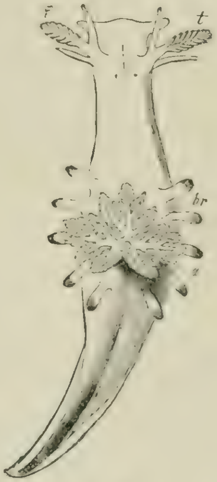

FIG. 163.

Ancula cristata, dorsal view. *a*, anus; *br*, pallial gill encircling the anus (external to these respiratory appendages are seen ten other club-like pallial appendages); *t*, posterior (branched) cephalic tentacle or rhinophore. (From Lankester, after Alder and Hancock.)

rhinophores very long, non-retractile; British. *Ancula*, Loven; mantle border scarcely distinguishable, without appendages; rhinophores branched; British (Fig. 163). *Doridunculus*, Sars. *Lamellodoris*, Alder and Hancock. *Ancylodoris*, Dybowsky, the only freshwater Nudibranch, from Lake Baikal, probably belongs to this family. Family 3. Heterodorididae, Fischer. No branchia. Genus—*Heterodoris*, Verrill and Emerton. Family 4. Dorididae, Gray. Mantle oval, covering the head and the greater part of the body; anterior tentacles ill developed; branchiae generally retractile. Genera—*Hexabranchus*, Ehrenberg; branchiae made up of separate fascicles, retractile within distinct cavities. *Doris*, Linnaeus; mantle elliptical, covering the whole body; branchiae tri- or quadri-pennatifid; British (Fig. 160, C). (Subgenera—*Archidoris*, Bergh. *Rostanga*, Bergh. *Aldisa*, Bergh. *Cadlina*, Bergh. *Jorunna*, Bergh. *Platydoris*, Bergh). *Chromodoris*, Alder and Hancock; body long and narrow; foot longer than the mantle; branchial plumes simply pinnate. Family 5. Doridopsidae, Alder. Pharynx suctorial; no radula; peri-branchial rosette on the dorsal surface, above the mantle border. Genus—*Doridopsis*, Alder and Hancock. Family 6. Corambidae, Bergh. Anus and branchia posterior below the mantle border. Genus—*Corambe*, Bergh (Fig. 164). Family 7. Phyllidiidae, Alder and Hancock. Pharynx suctorial; branchiae surrounding the body and placed between the mantle and the foot. Genera—*Phyllidea*, Cuvier; anus dorsal. *Fryeria*, Gray; anus posterior between the mantle and the foot.

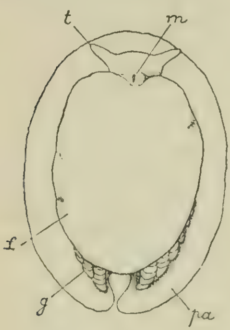

Fig. 164.

Corambe testudinaria, ventral aspect, magnified. *f*, foot; *g*, pallial gills; *m*, mouth; *pa*, "mantle"; *t*, tentacle. (After H. Fischer.)

The three last families constitute the sub-tribe "Porostomata," characterised by the reduction of the buccal bulb, which is transformed into a suctorial apparatus.

Tribe 3. Eolidomorpha (= Cladohepatica).

Nudibranchs in which the whole of the liver is contained in the integuments and the tegumentary papillae (Fig. 77). The genital duct is diaulic, and the male and female orifices are contiguous. A pair of laterally placed mandibles is present (Fig. 73, A). The anus is antero-lateral, except in the Proctonotidae, in which it is median. The tegumentary papillae are not ramified: they frequently contain terminal sacs (cnidosacs), which communicate on the one hand with the exterior, on the other hand with the digestive canal (Fig. 165). The cnidosacs contain nematocysts, which according to Wright and to Grosvenor are derived from the various species of Hydroids on which the animals feed. The nematocysts are invaginated while they are in the cnidosacs, but when expelled from them they are evaginated (Fig. 166). In some species of *Hedyle* and *Pseudovermis*, in which there are no tegumentary papillae, cnidosacs are found in the integuments; *e.g. Pseudovermis paradoxus* (Fig. 169).

FAMILY 1. EOLIDIDAE, d'Orbigny. Dorsal papillae spindle-shaped or club-shaped, each ending in an open sac of endodermic origin which communicates with a hepatic caecum and contains nematocysts. Genera—*Eolis*, Cuvier; the anterior angles of the foot prominent; rhinophores smooth; dorsal papillae compressed; British (Fig. 160, A). *Facelina*, Alder and Hancock; rhinophores foliated; radula triserial; British. *Tergipes*, Cuvier; rhinophores simple; radula uniserial; dorsal papillae in a single row on either side; otocyst with an otolith; British. *Gonieolis*, Bergh; no eyes. *Cuthona*, Alder and Hancock. *Embletonia*, Alder and Hancock. *Galvina*, Alder and Hancock. *Calma*, Alder and Hancock. *Hero*, Loven; a frontal velum; rhinophores simple; dorsal appendages in umbelliform clusters. FAMILY 2. GLAUCIDAE, Gray. The body furnished with three pairs of lateral lobes bearing the tegumentary papillae; foot very narrow; free-swimming pelagic forms. Genus — *Glaucus*, Forster. FAMILY 3. HEDYLIDAE, Bergh. Body elongated; the visceral mass marked off from the posterior part of the foot; dorsal tegumentary appendages absent or reduced to a single pair; spicules developed in the integument. Genus—*Hedyle*, Bergh (Fig. 168); from the Black Sea, Sea of Marmora, Mytilene, Flores. FAMILY 4. PSEUDOVERMIDAE, Pelseneer. Head devoid of tentacles; body elongated; the anus on the right side. Genus—*Pseudovermis*, Periaslavzeff (Fig. 169); from the Black Sea and Mytilene. FAMILY 5. PROCTONOTIDAE, Alder and Hancock. Anus situated posteriorly in the median line of the back; anterior tentacles atrophied; foot broad. Genera — *Janus*, Vérany; a median crest between the rhinophores; British. *Proctonotus*, Alder and Hancock; no intertantacular crest; British. FAMILY 6. DOTONIDAE, Adams. Bases of the rhinophores surrounded by a sheath; dorsal papillae club-shaped and more or less tuberculated, arranged in a single row on either side of the dorsum; no cnidosacs. Genera—*Doto*, Oken; a frontal veil; British. *Gellina*, Gray; no frontal veil. *Heromorpha*,

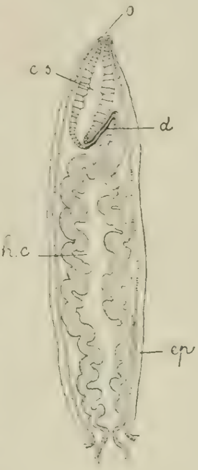

FIG. 165.

Sagittal section of a dorsal papilla of *Eolis*. *c.s*, cnidocystic sac; *d*, duct of junction between the hepatic caecum and the cnidocystic sac; *ep*, external epithelium; *h.c*, hepatic caecum.

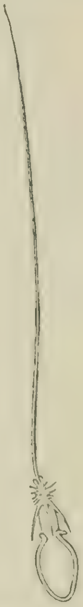

FIG. 166.

Evaginated cnidocyst from *Eolis punctata*, × 500. (After Vayssière.)

Bergh. Family 7. Fionidae, Alder and Hancock. Dorsal tegumentary papillae provided with a membranous expansion; liver in the form of two longitudinal canals into which the caeca of the dorsal papillae open; male and female orifices at some distance from one another; pelagic. Genus—*Fiona*, Hancock and Embleton. Family 8. Pleurophyllididae, Adams. Anterior tentacles in the form of a digging shield; mantle naked; tegumentary papillae or "branchiae" situated along the sides of the foot, beneath the mantle border. Genus—*Pleurophyllidia*, Meckel (Fig. 167). Family 9. Dermatobranchidae, Fischer. Like *Pleuro-*

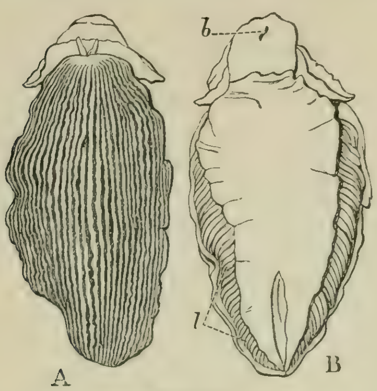

Fig. 167.

Pleurophyllidia lineata. *A*, dorsal view; *B*, ventral view. *b*, the mouth; *l*, lamelliform pallial gills (the posterior part of the foot bears a median glandular tract). (From Lankester, after Souleyet.)

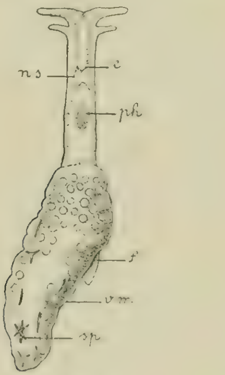

Fig. 168.

Hedyle glandulifera, dorsal aspect. *e*, eye; *f*, foot (posterior part); *n.s*, nervous system; *ph*, pharynx; *sp*, spicula; *v.m*, visceral mass. (After Kowalewsky.)

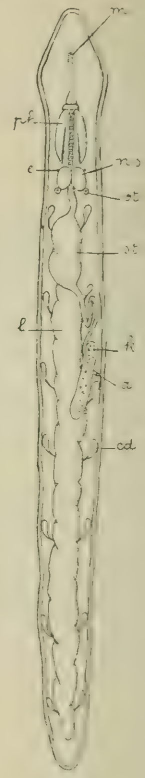

Fig. 169.

Pseudovermis paradoxus, dorsal aspect. *a*, anus; *cd*, cnidosac; *e*, eye; *k*, kidney; *l*, liver; *m*, mouth (on the ventral side, seen through the transparent head); *n.s*, nervous system; *ot*, otocyst; *ph*, pharynx; *st*, stomach. (After Kowalewsky.)

phyllidia, but wholly devoid of "branchiae." Genus—*Dermatobranchus*, van Hasselt.

TRIBE 4. ELYSIOMORPHA.

Nudibranchia in which the liver ramifies in the integuments and extends into the dorsal papillae. The genital duct is always triaulic, and the male and female orifices are distant (Fig. 105). The gonad is divided into spheroidal hermaphrodite lobules. There are no mandibles, and the radula is uniserial. There is never more than one pair of tentacles, and these are wanting in *Alderia* and some species of *Limapontia*. The otocysts contain each a single otolith.

FAMILY 1. HERMAEIDAE, Adams. Foot narrow; dorsal papillae without nematocysts, linear or fusiform, and disposed in several series. Genera—*Hermaea*, Loven; rhinophores split throughout their length; dorsal papillae linear; anus antero-dorsal; British. *Stiliger*, Ehrenberg; rhinophores simple; dorsal papillae fusiform or ovoid; anus antero-dorsal. *Alderia*, Allman; anus median and posterior; no tentacles; dorsal papillae linear; inhabitants of brackish waters; British. FAMILY 2. PHYLLOBRANCHIDAE, Bergh. Foot broad; dorsal papillae without nematocysts, flattened and foliaceous. Genera—*Phyllobranchus*, Alder and Hancock; foot simple; anus latero-dorsal. *Cyerce*, Bergh; ventral part of the foot divided transversely; anus median. FAMILY 3. PLAKOBRANCHIDAE, d'Orbigny. Body depressed, without dorsal papillae, but with two very large lateral expansions with dorsal plications; head flattened; eyes approximated. Genus—*Plakobranchus*, van Hasselt. FAMILY 4. ELYSIIDAE, Adams. Body elongated, with lateral expansions; head rounded and eyes separated; tentacles large; foot narrow. Genera—*Elysia*, Risso; British (Fig. 160, D, E). *Tridachia*, Deshayes. FAMILY 5. LIMAPONTIIDAE, Adams. No lateral expansions of the body and no dorsal papillae; body planariform; anus dorsal, median, and posterior. Genera—*Limapontia*, Johnston; no tentacles; head and body devoid of crests; British. *Actaeonia*, Quatrefages; head carinated laterally; British. *Cenia*, Alder and Hancock; head with two long tentacles (Fig. 170).

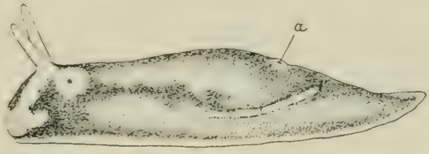

FIG. 170.

Cenia cocksi, left-side view, magnified *a*, anus. (After Hancock.)

ORDER 2. **Pulmonata**, Cuvier.

Euthyneura with a pallial cavity but no ctenidium. The pallial aperture is diminished by the fusion of the mantle border with the neck, and reduced to a comparatively small contractile orifice at its posterior extremity (Fig. 177, V). The pallial cavity and shell are often reduced ; the latter may be partially covered over, or internal, or even absent. There is never an operculum in the adult, except in *Amphibola*, and an operculum is only found during development in the Auriculidae, Siphonariidae, and Oncidiidae, all of which are marine forms. In the pallial cavity the interior wall of the mantle is traversed by vascular arborisations (Fig. 86, X), and thus constitutes a pulmonary organ adapted for breathing air. In the Janellidae the pulmonary cavity is prolonged into fine respiratory canaliculi (Fig. 90, *tr*), and thus becomes a tracheal lung. It is much reduced in the Oncidiidae, and in *Ancylus* and the Vaginulidae it disappears as a consequence of the complete abortion of the pallial cavity. In some rare cases the pulmonary cavity may be filled with water, and then its wall may give rise to a secondary branchia which is not the equivalent of a ctenidium (*Siphonaria*, Fig. 174, III). In other cases the inferior pallial lobe, situated beneath the pulmonary orifice of the Basommatophora, may be transformed into a branchia (Planorbidae, Figs. 89, *g*, and 175, *br*). The auricle of the heart is usually anterior (Fig. 86), as is the case in the most archaic Opisthobranchs, and it is only in the excessively detorted forms such as Testacella and the Oncidiidae that the ventricle lies in front of the auricle. The kidney usually has a more or less elongated duct or "ureter" (Stylommatophora, Fig. 86, V). In the nervous system, as a rule, all the ganglia are concentrated round the oesophagus and are closely apposed to one another (Fig. 146), but this is not the case in some archaic Basommatophora such as *Chilina*, *Auricula*, *Latia* (Fig. 96). In the Auriculid *Pythia*, the spermiduct retains the character of an open ciliated groove leading from the hermaphrodite aperture to the penial orifice (Fig. 171, *ci*): in other Auriculidae this groove is simply closed to form a canal extending from the hermaphrodite to the male orifice. In all other Pulmonates there is no longer a common genital orifice, but the hermaphrodite duct bifurcates to form a distinct oviduct of greater or less length, and the primitive hermaphrodite aperture becomes the female orifice. As a result of secondary changes, the orifices

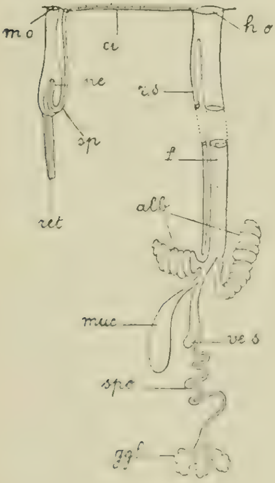

Fig. 171.

Reproductive apparatus of *Pythia*. *alb*, albuminiparous gland ; *ci*, ciliated groove ; *f*, fold in the distal part of the spermoviduct ; *g.gl*, ovo-testis ; *h.o*, hermaphrodite orifice ; *m.o*, male orifice ; *muc*, mucous gland ; *pe*, penis ; *ret*, retractor muscle of penis ; *r.s*, receptaculum seminis ; *sp*, spermiduct ; *spo*, spermoviduct ; *ve.s*, seminal vesicle. (After Plate.)

of the oviduct and penis may be approximated, a condition found in the majority of the Stylommatophora (Fig. 104).

The Pulmonates never have a free larval form; if a veliger is developed it is always contained in the egg membranes. The majority of Stylommatophora do not pass through a veliger stage, and in other forms the velum is almost always ill developed (Fig. 119, A, *ve*). The Pulmonates are for the most part aerial, but some live in fresh water, and others, but they are exceptional cases, are marine. The Pulmonates are distributed over the whole world, and include some seven thousand species, of which more than half belong to the genus *Helix*. Most of them enter into a resting stage during some part of the year; in the summer in hot climates, in the winter in cold climates. In our country the hibernation lasts for rather more than a third of the year.

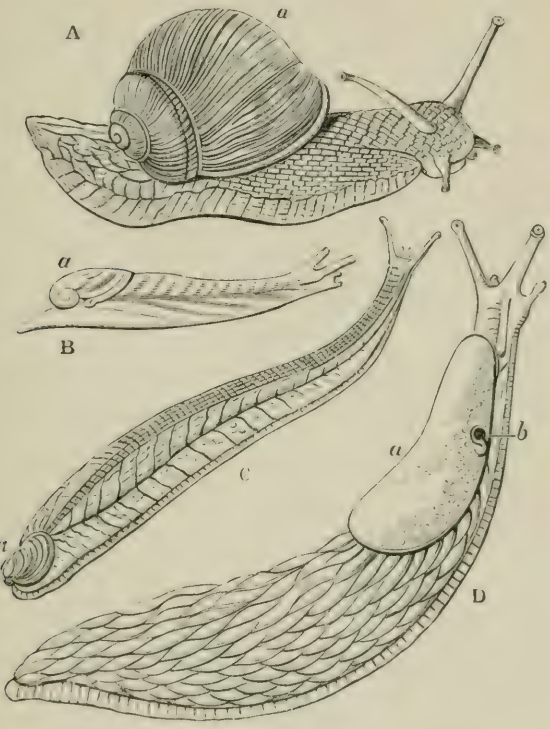

FIG. 172.

A series of Stylommatophorous Pulmonata, showing the reduction of the shell. *A*, *Helix pomatia*; *B*, *Daudebardia brevipes*; *C*, *Testacella haliotidea*; *D*, *Arion ater*. *a*, external shell in *A*, *B*, *C*; shell-sac (closed) in *D*; *b*, orifice of the pallial or pulmonary cavity. (From Lankester, after Férussac, Pfeiffer, and Reeve.)

The Pulmonata are divided into two sub-orders, Basommatophora and Stylommatophora; the former are generally aquatic, the latter terrestrial.

SUB-ORDER 1. BASOMMATOPHORA.

Testaceous Pulmonata with an external shell. The head bears a single pair of well-developed contractile but not invaginable tentacles, at the bases of which are the eyes (Fig. 107, I). The stomach, or at least a part of it, is very muscular. The penis is at some distance from the female aperture, except in *Amphibola* and *Siphonaria.* All have an osphradium (except the Auriculidae, which are terrestrial), which is situated outside the pallial cavity in those forms in which water is not admitted into the lung (*Limnaea*, *Planorbis*, Fig. 89, etc.). There is a veliger stage in the development, but the velum is reduced.

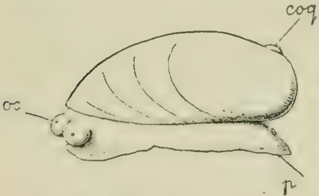

FIG. 173.

Otina otis, left-side view. *coq*, shell; *oc*, eye; *p*, foot.

FAMILY 1. AURICULIDAE, Blainville. Terrestrial and usually maritime animals; the genital duct monaulic, the penis being connected with the hermaphrodite opening by an open or closed groove (Fig. 171); shell with a prominent spire, the internal partitions often absorbed and the aperture denticulated. Genera—*Auricula*, Lamarck; foot not divided; tentacles swollen at their extremities; shell thick, oval, with an elongated aperture, and two folds on the columellar border. *Cassidula*, Férussac; foot not divided transversely, but bifid posteriorly; tentacles tapering; shell solid, umbilicated, with a short spire. *Alexia*, Leach; tentacles swollen and pigmented at their extremities; shell thin with a pointed spire, the exterior border of the aperture slightly thickened; British (Fig. 67). *Melampus*, Montfort; foot divided transversely and bifid behind; shell solid, with a short spire and a narrow aperture. *Carychium*, Müller; tentacles thick and short, with the eyes on the inside; shell small and short; the aperture oval with a denticulated internal border; terrestrial; British. *Scarabus*, Montfort; foot not divided; tentacles tapering; shell oval with a pointed spire, and a very constricted aperture, the margins bearing alternate teeth. *Leuconia*, Gray; foot divided; tentacles short and compressed; shell thin, oval, with a conical spire; aperture oval, the columellar border with a single fold; British. *Blauneria*, Shuttleworth; shell sinistral; aperture elongated, with a single columellar fold. *Pedipes*, Adanson; foot divided transversely; shell globular; the two borders of the aperture dentate; partitions not absorbed. FAMILY 2. OTINIDAE, Chenu. Shell with a short spire and a wide oval aperture; tentacles short. Genera—*Otina*, Gray; shell auriform; marine; British (Fig. 173). *Camptonyx*, Benson; shell conical with a spiral summit; terrestrial. FAMILY 3. AMPHIBOLIDAE, Adams. Visceral mass and shell spirally coiled; head broad, without prominent tentacles; foot short, operculated. Marine. Genus—*Amphibola*, Schumacher; from New Zealand. FAMILY 4. SIPHONARIIDAE, Adams. Visceral mass and shell conical ; tentacles atrophied ; head expanded ; genital orifices contiguous ; marine animals, with an aquatic pallial cavity containing secondary branchial laminae. Genera—*Siphonaria*, Sowerby (Fig. 174). *Hercynella*, Kayser ; from the Devonian. Family 5. Gadiniidae, Gray. Visceral mass and shell conical ; head flattened ; pulmonary cavity aquatic, but without a branchia ; genital orifices separated. Genus—*Gadinia*, Gray. Family 6. Chilinidae, Dall. Shell ovoid with a short spire, wide aperture, and folded columella ; tentacles broad and flattened ; inferior pallial lobe thick ; visceral commissure still twisted. Genus—*Chilina*, Gray ; rivers of Patagonia. Family 7. Limnaeidae, Broderip. Shell thin, dextral, with prominent spire and oval aperture ; tentacles angular and flat ; no inferior pallial lobe. Genera—*Limnaea*, Linnaeus (Fig. 107) ; shell wholly external, with a pointed spire ; British. *Amphipeplea*, Nillson ; shell in great measure covered by the mantle, globular, with a very short spire ; British. Family 8. Pompholygidae, Dall. Shell hyperstrophic (ultra-sinistral, that is to say, with an apparently dextral coil) with an obtuse spire ; the animal sinistral. Genera—*Pompholyx*, Lea ; tentacles dilated at their extremities ; shell depressed, the last whorl ventricose ; from California. *Choanomphalus*, Gerstfeldt ; shell umbilicated, with convex whorls ; tentacles slender ; Lake Baikal and California. Family 9. Planorbidae, Adams. Visceral mass and shell sinistrally coiled ; inferior pallial lobe very prominent and transformed into a branchia ; tentacles tapering. Genera — *Planorbis*, Guettard ; shell discoid ; branchia not folded (Fig. 89) ; British. *Bulinus*, Adanson ; shell ovoid with prominent spire ; branchia folded (Fig. 175). *Miratesta*, Sarasin. Family 10. Ancylidae, Menke. Shell conical, not spirally coiled ; tentacles short and compressed ; inferior pallial lobe

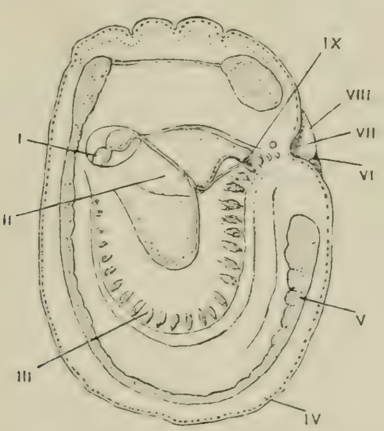

Fig. 174.

Siphonaria algesirae, removed from its shell. I, heart in the pericardium ; II, kidney ; III, pallial intrapulmonary gill ; IV, mantle ; V, columellar muscle ; VI, anus ; VII, pneumostome, to the left of which (in the pulmonary cavity) is the osphradial papilla ; VIII, inferior pallial lobe ; IX, renal pore.

transformed into a branchia. Genera—*Ancylus*, Geoffroy; no pulmonary cavity; animal dextral or sinistral; visceral commissure shortened; shell without internal septum; British (Fig. 176). *Latia*, Gray; a pulmonary cavity; visceral commissure long; shell with a posterior internal septum; from New Zealand. *Gundlachia*, Pfeiffer. FAMILY 11. PHYSIDAE, Dall. Visceral mass and shell sinistrally coiled; shell thin, with a narrow aperture; tentacles cylindrical; no inferior pallial lobe. Genera—*Physa*, Draparnaud; shell oval, partly covered by the edges of the mantle, which are divided into angular tags; British. *Aplexa*, Fleming; shell with a pointed spire; edges of the mantle not divided and very slightly reflected over the shell; British.

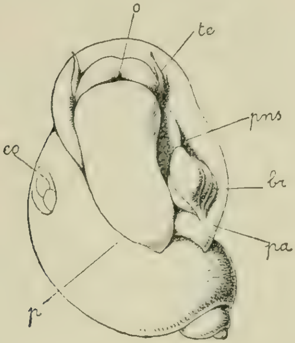

FIG. 175.

Bulinus tabulatus, ventral aspect. *br*, pallial extrapulmonary gill; *co*, heart; *o*, mouth; *p*, foot; *pa*, mantle; *pns*, pneumostome; *te*, tentacle.

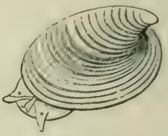

FIG. 176.

Ancylus fluviatilis, dorsal view. To the left, the head with the two cephalic tentacles. (From Lankester, after Reeve.)

SUB-ORDER 2. STYLOMMATOPHORA.

Pulmonata with two pairs of tentacles (except the Janellidae and *Vertigo*, which have only a single pair); these tentacles are invaginable, and the eyes are borne on the summits of the posterior pair. The male and female genital orifices open into a common vestibule except in the Ditremata (Vaginulidae and Oncidiidae). A suprapedal gland is present in nearly all the groups. With the exception of *Oncidium*, there is no longer a veliger stage in the development; the embryo is often furnished with a contractile pedal vesicle (Fig. 117).

The Stylommatophora may be divided into four tribes: the Holognatha, Agnatha, Elasmognatha, and Ditremata.

TRIBE 1. HOLOGNATHA.

Jaw simple, without a superior appendage.

FAMILY 1. SELENITIDAE, Fischer. Radula with elongated and pointed teeth, like those of the Agnatha; a jaw present. Genera—*Selenites*, Fischer; shell external, depressed, widely umbilicated. *Plutonia*, Stabile; animal limaciform, with flattened internal shell and a posterior pulmonary aperture. *Trigonochlamys*, Böttger; no shell. FAMILY 2. ZONITIDAE, Pilsbry. Shell external, smooth, heliciform or flattened; radula with pointed marginal teeth. Genera—*Zonites*, Montfort; shell depressed, wholly external; British. *Ariophanta*, Desmoulins;

mantle produced anteriorly into a cervical lobe; foot with a posterior dorsal mucous pore. *Orpiella*, Gray; differs from *Ariophanta* in having a horn-shaped protuberance at the hinder extremity of the foot. *Vitrina*, Draparnaud; the mantle projects in front and on the right side, and partially overlaps the thin and depressed shell; foot elongated, without a posterior mucous pore; British. *Helicarion*, Férussac; differs from *Vitrina* in having the foot truncated anteriorly, with a posterior mucous pore. FAMILY 3. LIMACIDAE, Gray. Shell almost completely covered by the mantle, or internal. *Parmacella*, Cuvier; shell unguiform with a spiral summit; the mantle occupies the centre of the body and completely covers the shell except for a very small orifice above the spire. *Limax*, Linnaeus; shell wholly internal, without a spiral summit; mantle reduced, and situated on the anterior part of the body; pulmonary aperture towards the hind end of the pallial border; British. *Urocyclus*, Gray; shell oval, without a spire, internal except for a small median orifice in the hinder part of the mantle; pulmonary aperture in the middle of the pallial border; African. *Parmarion*, Fischer. *Amalia*, Heynemann. *Agriolimax*, Mörch. *Mesolimax*, Pollonera. *Monochroma*, Simroth. *Paralimax*, Böttger. *Metalimax*, Simroth. FAMILY 4. PHILOMYCIDAE, Fischer. No shell; the mantle covers the whole surface of the body; radula with squarish teeth. Genus—*Philomycus*, Férussac; foot broad; genital orifice near the right tentacle. FAMILY 5. OSTRACOLETHIDAE, Simroth. Shell largely chitinous, not spiral, its calcareous summit projecting through a small hole in the mantle which elsewhere covers it. Genus—*Ostracolethe*, Simroth. FAMILY 6. ARIONIDAE, Gray. Shell internal or absent; animal limaciform; mantle restricted to the anterior and middle part of the body; radula with squarish teeth. Genera—*Arion*, Férussac; respiratory orifice at the anterior end of the pallial border; genital orifice close to the respiratory orifice; shell reduced to simple isolated calcareous granules; British (Fig. 172, D). *Geomalacus*, Allmann; shell internal, oval; Ireland. *Ariolimax*, Mörch. *Anadenus*, Mörch. FAMILY 7. HELICIDAE, Gray. Shell with medium spire, external or partially covered by the mantle; mandible folded; radula with square teeth; genital orifice below the right posterior tentacle; genital apparatus generally provided with a dart-sac and multifid vesicles. Genera—*Helix*, Linnaeus; shell globular, conical or depressed, with a rounded or expanded aperture (Figs. 172, A and 177); British. (A large number of sub-genera has been established, which includes more than 4000 species: *Polygyra*, Say. *Sagda*, Beck. *Pleurodonta*, Fischer von Waldheim. *Helicodonta*, Férussac. *Helicophanta*, Beck. *Acavus*, Montfort. *Sitala*, Adams. *Chlorites*, Beck. *Hapalus*, Albers, etc.) *Bulimus*,

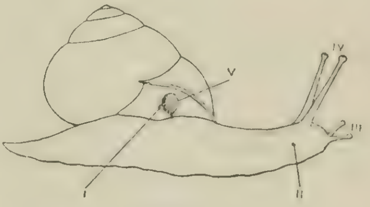

FIG. 177.

Helix nemoralis, right-side view. I, anus; II, genital (hermaphrodite) pore; III, anterior tentacles; IV, posterior (oculiferous) tentacles; V, pneumostome in its maximum distension.

Scopoli ; shell ovoid, with oval or elongated aperture and a thickened border. *Hemphillia*, Binney and Bland ; shell unguiform, its edges covered by the mantle ; North America. *Berendtia*, Crosse and Fischer. *Cochlostyla*, Férussac. *Rhodea*, Adams. Family 8. Endodontidae, Pilsbry. Shell spiral, external, generally ornamented with ribs ; borders of the aperture thin and not reflected ; radula with square teeth ; genital ducts without accessory organs. Genera—*Endodonta*, Albers. *Punctum*, Morse. *Sphyradium*, Charpentier. *Laoma*, Gray. *Pyramidula*, Fitzinger. Family 9. Orthalicidae, Fischer. Shell external, ovoid, the last whorl swollen, the aperture oval, with a simple border ; radular teeth in oblique rows. Genus—*Orthalicus*, Beck ; American. Family 10. Bulimulidae. Fischer ; jaw formed of folds imbricated externally and meeting at an acute angle near the base. Genera—*Bulimulus*, Leach ; shell elongated, oval, external. *Peltella*, Webb and van Beneden ; shell auriform, internal. *Amphibulimus*, Montfort. Family 11. Cylindrellidae, Fischer. Shell turriculated, with numerous whorls, the last whorl more or less detached. Genus—*Cylindrella*, Pfeiffer ; aperture circular, with reflected peristome ; summit commonly truncated ; America. Family 12. Pupidae, Fleming. Shell external, with elongated spire and numerous whorls ; aperture generally narrow ; male genital duct without multifid vesicles. Genera—*Pupa*, Lamarck ; shell cylindrical, dextral with obtuse summit ; aperture parallel to the axis, small and contracted ; British. *Eucalodium*, Crosse and Fischer ; shell turriculated, the summit truncated, the aperture oval. *Vertigo*, Müller ; shell small, ovoid, the summit obtuse, the aperture small and contracted by numerous teeth ; dextrally or sinistrally coiled ; a single pair of tentacles ; British. *Buliminus*, Ehrenberg ; shell umbilicated, ovoid, with elongated aperture and a simple columella ; British. *Clausilia*, Draparnaud ; shell turriculated, sinistral ; aperture oval ; the columella with corrugations and a movable piece, the clausilium, by means of which the mouth of the shell can be closed ; British. *Balea*, Prideaux ; shell sinistral, differs from *Clausilia* in the absence of columellar corrugations and clausilium. *Zospeum*, Bourguignat ; no eyes, shell short and dextral. *Megaspira*, Lea. *Strophia*, Albers. *Anostoma*, Fischer. Family 13. Stenogyridae, Fischer. Shell elongated, with a more or less obtuse summit ; aperture oval with a simple border. Genera—*Achatina*, Lamarck ; shell ovoid, the spire conical, the last whorl ventricose ; the columella twisted. *Stenogyra*, Shuttleworth ; shell turriculated ; the whorls numerous, increasing slowly (Fig. 8). *Ferussacia*, Risso ; shell small, thin, and brilliant ; aperture elongate, oval ; British. *Caecilianella*, Férussac ; shell cylindrical, the spire elongated, the columella truncated ; eyes absent ; subterranean in habit ; British. *Cionella*, Jeffreys. *Azeca*, Leach. *Opeas*, Albers. *Rhodea*, Adams. Family 14. Helicteridae, Fischer. Shell bulimoid, dextral or sinistral ; radular teeth narrow at their bases, expanded at their extremities and multicuspidate. Genera—*Helicter*, Férussac. *Tornatellina*, Beck.

Tribe 2. Agnatha.

No jaws ; the radular teeth narrow and pointed ; carnivorous. This group is possibly polyphyletic.

Family 1. Oleacinidae, Adams. Shell oval, elongated, with a narrow aperture; neck very long; labial palps prominent. Genera—*Oleacina*, Bolton (= *Glandina*); aperture truncated anteriorly; columella smooth. *Streptostyla*, Shuttleworth; columella with a fold; aperture elongate, not truncated anteriorly. Family 2. Testacellidae, Gray. Shell globular or auriform, external or partly covered by the mantle. Genera—*Streptaxis*, Gray; shell external, heliciform, the last whorls generally set obliquely to those first formed. *Gibbulina*, Beck; shell cylindrical, umbilicated. *Aerope*, Albers; shell external, globular, with a small umbilicus; radular sac enormous; from South Africa. *Rhytida*, Albers; shell depressed, with a very wide umbilicus; from New Zealand. *Daudebardia*, Hartmann; shell coiled, only occupying the posterior part of the body; animal limaciform; the genital orifice situated between the right tentacle and the shell (Fig. 172, B). *Testacella*, Cuvier (Fig. 172, C); shell small, auriform, situated at the posterior extremity of the limaciform body; genital orifice near the right tentacle. *Chlamydophorus*, Binney; shell plate-shaped and nearly completely covered by the mantle. *Schizoglossa*, Hedley. Family 3. Rathouisiidae, Heude. Animal naked, devoid of a shell, with a carinated mantle covering the whole body; male and female orifices distant; the female orifice near the anus. Genera—*Rathouisia*, Heude. *Atopos*, Simroth.

Tribe 3. Elasmognatha.

The jaw with a well-developed dorsal appendage.

Family 1. Succineidae, Chenu. Anterior tentacles much reduced; male and female orifices contiguous but distinct; shell thin, spiral, with a short spire. Genera—*Succinea*, Draparnaud; shell external, oblong, with a large aperture; British. *Homalonyx*, d'Orbigny; shell auriform, the spire scarcely projecting; the edges of the shell covered by the mantle; animal limaciform; American. *Hyalimax*, Adams; shell oval, wholly internal. *Neohyalimax*, Simroth. Family 2. Janellidae, Gray. Limaciform animals, with an internal rounded shell; the mantle very small and triangular; the pulmonary chamber with tracheae; no anterior tentacles. Genera—*Janella*, Gray. *Aneitella*, Cockerell. *Aneitea*, Gray (Fig. 178). *Triboniophorus*, Humbert. All from the Australo-Zelandic region.

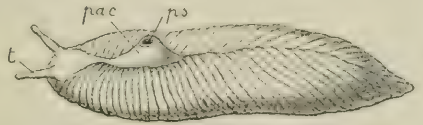

Fig. 178.

Aneitea macdonaldi, Gray, left-side view. *pa.c*, pallial cavity; *ps*, pneumostome; *t*, tentacle. (After MacDonald.)

Tribe 4. Ditremata.

Male and female genital orifices distant (Fig. 59, *o.f*, *o.m*).

Family 1. Veronicellidae, Gray. Terrestrial, naked, limaciform animals, without a shell; the female orifice on the right in the middle of the body; the anus posterior. Genus—*Vaginula*, Férussac (Fig. 179). Family 2. Oncidiidae, Philippi. Limaciform naked marine animals, without a shell; female orifice near the anus, at the posterior end of the body; a reduced pulmonary cavity with a distinct pneumostome (Fig. 59, *pns*). Genera—*Oncidium*, Buchanan; body elongated and narrow; penis with accessory apparatus; from the Indian Ocean. *Oncidiella*, Gray; body oval; mantle thick, with an emarginated border; penis without accessory apparatus; British (Fig. 59). *Peronia*, Blainville; body oval; the mantle covered with ramified appendages and oculiferous tubercles.

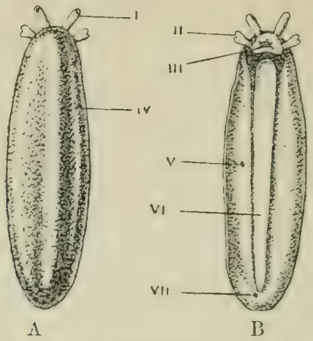

Fig. 179.

Vaginula luzonica. *A*, dorsal aspect; *B*, ventral aspect. I, posterior tentacle; II, anterior tentacle; III, mouth; IV, mantle; V, female orifice; VI, foot; VII, anus. (After Souleyet.)

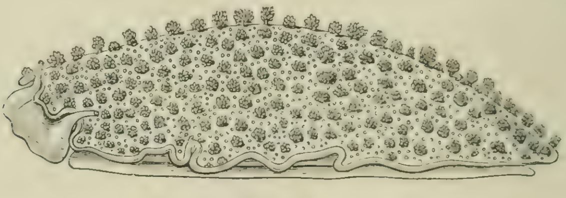

Fig. 180.

Oncidium tonganum, left-side view. (From Lankester, after Quoy and Gaimard.)

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CHAPTER IV

THE SCAPHOPODA

CLASS III.—SCAPHOPODA, Bronn
(= Solenoconcha, de Lacaze-Duthiers).

Definition.—Marine bilaterally symmetrical Prorhipidoglossomorpha; the body and shell elongated along the antero-posterior axis and nearly cylindrical. The right and left margins of the mantle are united ventrally and thus form a complete tube surrounding the body, but with an anterior and a posterior aperture. The head is somewhat rudimentary and devoid of eyes, but bears two dorsal appendages furnished with numerous long filaments (Fig. 183, I). The foot is cylindrical and adapted to digging. A radula is present, but there is no ctenidium. The sexes are separate.

Historical.—These animals were formerly mistaken for tubicolous Annelids, and afterwards were classed among the Gastropoda, near *Fissurella*. Blainville, in 1819, was the first to rank them as a distinct order of Gastropoda under the name "Cirrhobranchia." In 1857 de Lacaze-Duthiers, as the result of a careful anatomical investigation, created the division Solenoconcha to receive *Dentalium*, making his new division equivalent to Lamellibranchia, and including the two groups, together with the Brachiopoda, in a class Acephala. Since de Lacaze-Duthiers' memoir, the Solenoconcha have been universally recognised as a division equivalent to the Lamellibranchia and Gastropoda, but the name Scaphopoda, proposed by Bronn in 1862, has been more generally used for the sake of uniformity. More recent investigations, however, have shown that the Scaphopoda are more nearly akin to the Gastropoda than to the Lamellibranchia.

I. General Description and External Characters.

The shell (Figs. 181, D, E and 186) has the form of a very elongated cone, slightly curved, the concavity of the curve being dorsal: it is capable of containing the entire animal. The larger orifice of the shell and subjacent mantle is morphologically the anterior or cephalo-pedal aperture. Near the smaller posterior aperture the shell, being older, is also thicker. The anterior aperture of the mantle has a conspicuously thick border. The posterior aperture is emarginated by a ventral sinus and is furnished interiorly with a dorsal and a ventral valve, which are capable of being applied to one another. The animal lives buried obliquely in the sand, only the posterior extremity projecting into the water, and therefore it is the posterior aperture that is at once inhalant and exhalant and serves for the expulsion of the excrements and the genital products. In the extended state of the animal the foot and cephalic tentacular filaments project from the anterior opening.

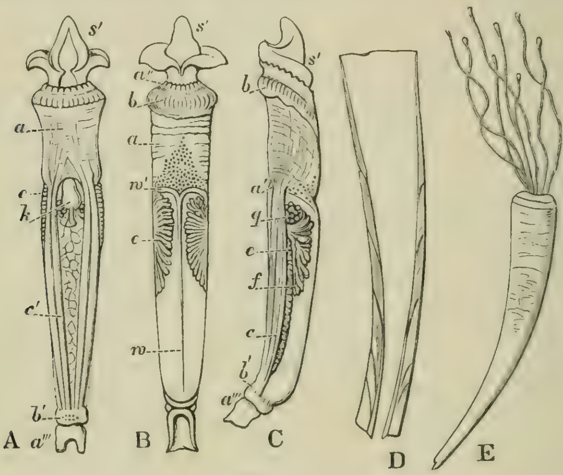

FIG. 181.

Dentalium vulgare. *A*, ventral view of the animal removed from its shell; *B*, dorsal view of the same; *C*, right-side view of the same; *D*, the shell in section; *E*, right-side view of the animal in its shell, with cephalic appendages (captacula) exserted as in life. *a*, mantle; *a′*, longitudinal retractor muscle; *a″*, fringe surrounding the anterior opening of the mantle-chamber; *a‴*, the posterior appendix of the mantle; *b*, anterior circular muscle of the mantle; *b′*, posterior circular muscle of the mantle; *c*, *c′*, longitudinal retractor muscle; *e*, liver; *f*, gonad; *k*, buccal mass (seen through the mantle); *q*, left kidney; *s′*, anterior extremity of the foot; *w*, *w′*, longitudinal blood-sinus of the mantle. (From Lankester, after Lacaze-Duthiers.)

The pallial cavity extends continuously from one aperture to the other. In the middle and posterior regions of the body the liver, the gonads, and even the kidneys, extend into the mantle and may increase its thickness to such an extent that the pallial cavity is reduced to a rather narrow canal (Siphonopodidae).

The head is situated at the anterior end of the body on the concave or dorsal side. In shape it is a sort of cylindrical projection or proboscis, and is contractile but not invaginable. In the Dentaliidae its anterior aperture is surrounded by eight palps or lobes with scalloped margins, but in the Siphonopodidae it is flattened and devoid of palps (Fig. 183, VI). Laterally and posteriorly it is provided with two pouches, and quite at its posterior end, on either side of its dorsal surface, are two broad, symmetrical, and flattened tentacular lobes (Fig. 183, IV) which appear to be homologous with the cephalic lobes of Rhipidoglossa (Fig. 130, II). The cephalic filaments or "captacula" (Fig. 181, E) are inserted on the margins of these lobes, and when extended, radiate in all directions from them (Figs. 182, *ca*; 183, I).

These captacula are of unequal length, autotomous, and capable of regeneration: they are ciliated, highly contractile, and their extremities are swollen and club-shaped, with a small lateral concavity in each. These organs are in the first instance tactile, but also prehensile. The difference in their length is the result of their regeneration after being lost.

The foot has the form of an elongated cylinder, is very extensible, and when forcibly projected beyond the aperture of the shell, serves as a digging organ. In the Dentaliidae it is pointed in front, but has an oblique wing-shaped fold or pleat on either side of its free extremity: these two folds are contiguous on the ventral but interrupted on the dorsal side. In the Siphonopodidae the foot ends in a retractile disc with papillated margins (Fig. 183, VIII), and in *Pulsellum* there is a filiform tentacle in the middle of the disc. The powerful retractor muscles of the foot form two symmetrical bundles inserted far back on the dorsal side of the shell (Fig. 181, *r*)

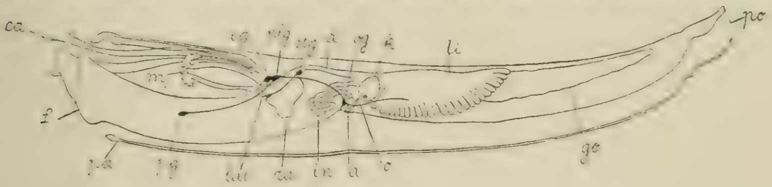

FIG. 182.

Diagram of the organisation of *Dentalium*, left-side view. *a*, anus; *ca*, captacula; *c.g*, cerebral ganglion; *f*, foot; *go*, gonad; *in*, intestine; *k*, left kidney; *la.c*, labial commissure; *li*, liver; *m*, mouth; *o*, orifice leading into the perianal sinus; *oe*, oesophagus; *pa*, mantle; *p.g*, pedal ganglion, with otocyst; *pl.g*, pleural ganglion; *po*, posterior orifice of the mantle; *ra*, radular sac; *st.g*, stomato-gastric ganglion.

II. ANATOMY.

1. *Alimentary Canal.*—The non-invaginable proboscis (Fig. 183, V, VI) leads directly into a true buccal cavity situated in the trunk at the base of the foot (Fig. 182, *f*). In the interior of this buccal cavity there is an azygos dorsal mandible and a ventral radula. The radular sac is short, but its muscles and cartilages are powerful and form a buccal mass of large size. The radula is short and arcuate, with five teeth in each transverse row, the formula being

1.1.1.1.1 (Fig. 2, C). The central tooth is simple and subquadrangular; the laterals stout and subtrigonal, tricuspidate, with wide bases and reflected borders; the marginals have the form of subquadrangular non-denticulate transverse plates.

The oesophagus is rather short and is provided with two large lateral symmetrical pouches, directed ventralwards; these correspond to the oesophageal pouches of the Polyplacophora and Aspidobranchia.

The stomach is nothing more than the most posterior bend of the digestive canal (Fig. 182). It presents a small posterior ciliated pyloric caecum, and receives the ducts of the liver. The last-named organ is situated behind the stomach and the rest of the alimentary canal. It is made up of radiating caeca (Fig. 182, *li*), gathered into two lobes which extend into the sides of the mantle, and open right and left into the so-called stomach or posterior bend of the alimentary canal. Though the two liver lobes are symmetrical in the Dentaliidae, they are no longer so in *Siphonodentalium*. In this genus the principal mass of the liver lies in front of the gonad and is continued posteriorly into two long parallel caeca extending to the extremity of the body; the organ has no longer an apparent symmetry, but all its radiating caeca are directed to the left side and open into the "stomach" by a single orifice.

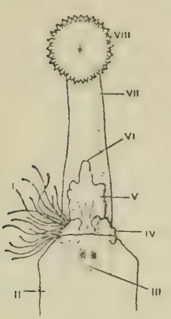

FIG. 183.

Siphonodentalium, anterior end of body, dorsal view. I, captacula; II, mantle; III, radular mass; IV, right tentacular lobe, without the captacula; V, buccal pouch; VI, mouth; VII, foot; VIII, terminal foot-disc.

The intestine bends forward (Fig. 182, *in*) and forms several loops, all of which lie in the anterior part of the body, near the buccal mass, and finally opens in the mid-ventral line behind the visceral commissure. In the Dentaliidae there is an anal gland on the right side of the rectum (Fig. 182, *a*).

2. *Circulatory Apparatus*.—The structure of the circulatory system is exceedingly simple. There are no differentiated vessels, not even a ventricle with well-developed muscular walls. At the most there is a more contractile portion of the blood-system in the neighbourhood of the anus, but it has no afferent or efferent vessels, and is continuous with the rest of the blood-spaces. These latter are sinuses, without an endothelial lining, distributed between the organs in the different parts of the body. The principal sinuses are: the perianal, the pedal, the visceral, and the pallial. It is in the last-named that the anterior dorsal and ventral portions are more clearly defined and have something of the appearance of vessels. Two buttonhole-shaped orifices, situated near the renal apertures, place the perianal sinus in communication with the external medium and

admit of the expulsion of blood during violent contractions of the body (Fig. 182, *o*). There is no specialised respiratory apparatus. Respiration is effected by the internal surface of the mantle, particularly by the anterior ventral region.

3. *Excretory Organs.*—The Scaphopoda have two symmetrical kidneys, situated in front of the gonad on the ventral side of the middle of the body (Figs. 181, *q*, and 182, *k*). They have the form of two short but fairly wide sacs with pleated walls, lying between the intestinal mass and the stomach. They have no communication with one another and have no reno-pericardial duct. They open to the exterior on either side of the anus.

4. *Nervous System and Sense Organs.*—The nervous system of the Scaphopoda comprises the same four pairs of principal nerve ganglia as are found in the Gastropoda and Lamellibranchia, in addition to the stomato-gastric system. The cerebral ganglia are joined to one another and are situated on the dorsal side of the oesophagus: they innervate the proboscis with its palps and the tentacular lobes and captacula. Each cerebral ganglion is in close juxtaposition to the corresponding pleural ganglion (Fig. 182, *c.g*, *pl.g*), which innervates the mantle. The cerebral and pleural ganglia are united to the pedal ganglion of the same side by a long connective which is apparently single in the distal part of its course, but bifurcates just before it reaches the cerebral and pleural ganglia, sending a branch to each. The two pedal ganglia are situated in the foot (Fig. 182, *p.g*) and are attached to one another.

The visceral commissure takes its origin from the pleural ganglia. It is rather long, and bears on the posterior part of its course two symmetrical visceral centres (Fig. 182, *v.g*) in the form of simple and ill-defined ganglionic swellings, lying on either side of the anus close beneath the tegumentary epithelium, and thus resembling the visceral ganglia of the Lamellibranchia. These two centres are united by a commissure passing in front of the rectum.

From the cerebral ganglia there arises—as in many other Molluscs—an infra-oesophageal labial commissure (Fig. 182, *la.c*), bearing a ganglion on either side, from which a branch of the stomato-gastric commissure properly so called (Fig. 182, *st.g*) is given off, as is the case in the Polyplacophora, Aspidobranchia, and Cephalopoda. The stomato-gastric commissure passes to the ventral side of the oesophagus, between it and the buccal bulb, and bears two or four symmetrical ganglia on the middle of its course. The labial commissure also gives off a nerve on each side, which passes to the subradular organ and terminates below it in a ganglion.

The Scaphopoda have only three differentiated sensory organs: the captacula or tentacular filaments, the subradular organ, and the otocysts. The tentacles, which are seemingly tactile and olfactory organs, are dorsal in position and have the form of flattened lobes

(Fig. 183, IV), on which the numerous filiform appendages or captacula are inserted. The extremity of each captaculum is swollen and club-shaped with a small lateral pit, and contains a terminal ganglion and a system of ganglion cells whose prolongations are continued into neuro-epithelial elements situated in the lateral pit. The subradular organ is a ciliated ridge on the ventral side of the buccal cavity opposite to the mandible. The epithelium of this ridge contains nerve end-cells, and beneath it are two small nerves derived from the labial commissure, each ending in a small ganglion. The otocysts are situated in the foot (Fig. 182) on the posterior face of the pedal ganglia. They are innervated from the cerebral ganglia and each contains numerous otoconia.

5. *Reproductive Organs.*—The sexes are always separate. The gonad is unpaired and median, and is extremely long, occupying the whole of the postero-dorsal region of the body, below the retractor muscles (Figs. 181, *f* and 182, *go*). It is divided into symmetrical transverse lobes, and its anterior extremity is contracted to form a duct, which diverges to the right and opens into the right kidney, as in the Aspidobranchia.

III. EMBRYOLOGY.

The ova are laid singly, and undergo irregular segmentation immediately after fertilisation. The ectodermic cells multiply much more rapidly than the large endodermic cell or entomere, which remains for some time unsegmented (Fig. 184, *ma*). Finally, the entomere segments in its turn, and the endodermic cells derived from it are invaginated to form a gastrula with a large blastopore, situated at the posterior extremity. The embryo elongates and acquires an anterior apical tuft of cilia (Fig. 15, *fl*), behind which at first two and afterwards three, or sometimes four, parallel ciliated rings are formed. These ciliated rings constitute the locomotory velum, and their number diminishes in proportion as the velum, which is more or less reflected backwards over the body, becomes more prominent (Fig. 185, III).

The blastopore remains open, and gradually travels along the ventral side towards the anterior extremity of the larva. A shallow shell-gland is formed on the dorsal side and extends right and left over the whole dorsal surface, forming two lateral, parallel, and symmetrical pallial lobes which extend ventrally and finally unite together (Fig. 185, II). In this manner the tubular mantle is formed round the body. The shell secreted by the mantle is at first cupuliform, but subsequently, like the mantle itself, becomes tubuliform as the result of the fusion of its lateral margins (Fig. 119, B). The expanded embryonic shell may still be seen at the initial extremity in some specimens of *Siphonodentalium.*

The pedal prominence arises on the ventral surface and grows forward; after the disappearance of the larval velum the foot is used for creeping. The cerebral ganglia arise as two deep symmetrical ectodermic invaginations in the velar area. The otocysts are formed as invaginations of the surface of the foot, and the pedal ganglia originate after the otocysts from thickenings of the ectoderm. The endodermic cavity gives rise to the stomach and intestine. The liver is developed in connection with the wall of the stomach. The anal opening is not formed till a very late period. At the end of five or six days the velum atrophies, the young animal ceases to swim and begins to crawl along the sea bottom.

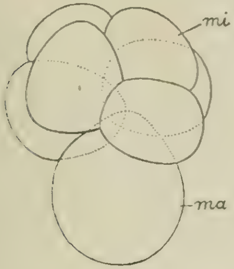

FIG. 184.

Embryo of *Dentalium*, with six micromeres or ectodermic cells and a single macromere or endodermic cell. *ma*, macromere; *mi*, micromere. (After Kowalewsky.)

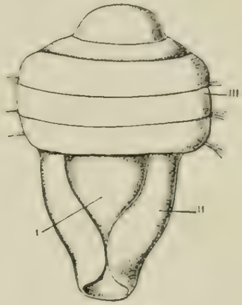

FIG. 185.

Larva of *Dentalium*, aged one and a half day; ventral aspect. I, foot; II, mantle; III, velum forming a sort of test. (After Kowalewsky.)

IV. BIONOMICS AND DISTRIBUTION.

The Scaphopoda are marine burrowing molluscs, and as a rule only allow the posterior extremity to project from the sand in which they hide themselves. They feed on the lowest organisms, Diatomacea, Protozoa, etc.

There are 150 living and nearly 275 fossil species of Scaphopoda. The living forms are distributed throughout all seas from the littoral to a depth of 2500 fathoms. The fossil species extend back to the middle Silurian, but are most abundant from the Cretaceous onwards.

V. REVIEW OF THE FAMILIES OF SCAPHOPODA.

There are two different types in this homogeneous group, but the differences between them are not of more than family value.

FAMILY 1. DENTALIIDAE, Gray. Foot conical with a laterally expanded and dorsally interrupted encircling sheath. Shell tubular, curved, with the greatest diameter at the anterior aperture, and tapering evenly to the posterior aperture. Genera—*Dentalium*, Linnaeus; posterior orifice of the shell truncated, entire, without an incision or accessory tube. *Antalis*, Adams; posterior orifice with a short incision. *Fissidentalium*, Fischer; posterior extremity with a long fissure on the ventral side; abyssal. *Fustiaria*, Stoliczka. *Schizodentalium*, Simroth; ventral border of the posterior aperture with a series of small holes arranged in a straight line. *Heterochisma*, Simroth.

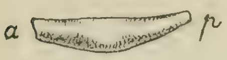

Fig. 186.

Cadulus gracilis, Jeffreys, shell, left view. *a*, anterior orifice; *p*, posterior orifice. (After Watson.)

Family 2. Siphonopodidae, Simroth. Foot expanded distally into a symmetrical disc, with a crenate continuous edge (Fig. 183) or simple and vermiform without well-developed lateral processes; shell often contracted towards the anterior aperture. Genera—*Siphonodentalium*, Sars; foot ending in a median disc without a median appendage. *Cadulus*, Philippi (Fig. 186). *Dischides*, Jeffreys. *Pulsellum*, Sars; terminal disc of the foot with a median appendage. *Entalina*, Monterosato.

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CHAPTER V

THE LAMELLIBRANCHIA

CLASS IV.—THE LAMELLIBRANCHIA, Blainville

(= Acephala testacea, Cuvier; Conchifera, Lamarck; Pelecypoda, Goldfuss; Lipocephala, Ray Lankester).

Order 1. **Protobranchia.**
  Sub-Order 1. **Solenomyacea.**
  ,, 2. **Nuculacea.**

Order 2. **Filibranchia.**
  Sub-Order 1. **Arcacea.**
  ,, 2. **Trigoniacea.**
  ,, 3. **Mytilacea.**
  ,, 4. **Pectinacea.**
  ,, 5. **Dimyacea.**

Order 3. **Eulamellibranchia.**
  Sub-Order 1. **Ostraeacea.**
  ,, 2. **Submytilacea.**
  ,, 3. **Tellinacea.**
  ,, 4. **Veneracea.**
  ,, 5. **Cardiacea.**
  ,, 6. **Chamacea.**
  ,, 7. **Myacea.**
  ,, 8. **Adesmacea.**
  ,, 9. **Anatinacea.**

Order 4. **Septibranchia.**
  Sub-Order. **Poromyacea.**

Definition.—The Lamellibranchia are Molluscs with an internal and external symmetry. The cephalic region is rudimentary, and the mantle, divided into a right and a left lobe, secretes a bivalve shell which covers and encloses the whole body. The cephalic region is only furnished with a pair of labial palps on each side. The foot is ventral, generally adapted to burrowing and without a plantar surface. The two pallial lobes are united by one or two transverse muscles which close the two valves of the shell. There are two lateral and symmetrical ctenidial branchiae under the mantle; their distal extremities are directed posteriorly and their filaments may exhibit an extreme degree of concrescence, either among themselves or with the mantle or with the visceral mass.

I. General Description and External Characters.

The mantle consists of two thin tegumentary lobes attached to the trunk dorsally, and extending over the sides to the ventral surface so far that they can be brought together below the foot. Thus the whole of the animal's body may be covered by the mantle. In structure, the mantle is normally rather thin, and there is only some connective tissue and a few muscular fibres between the internal and external layers of epithelium. In some few cases the gonads may extend into the mantle: into both lobes in the Mytilidae, into the right lobe only in the Anomiidae. The internal surface may present glandular modifications, of which the most important are the hypobranchial glands characteristic of the Protobranchia: they are situated posteriorly beyond the gills. The margins of the mantle normally present reduplications, generally three in number (Fig. 187, *pa'*, *pa''*, *pa'''*), and in the Pectinidae the most internal of the three is turned inwards to form the "velum" (Fig. 235). The margins of the mantle of Lamellibranchs are frequently furnished with glands, pigment spots, and various sensory organs in the form of tentacles, and even of eyes. The pigmentation of the pallial border is due to the combined action of the light and the oxygen of the surrounding medium, and is most conspicuous at those points where the respiratory fluid enters the pallial cavity.

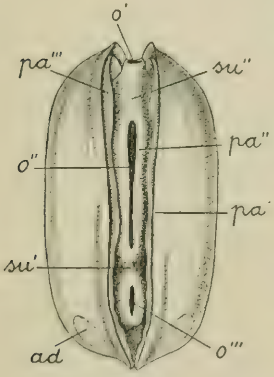

Fig. 187.

Kellya suborbicularis, Montagu, without the shell, ventral aspect. *ad*, posterior adductor; *o'*, inhalant orifice; *o''*, pedal orifice; *o'''*, exhalant orifice; *pa'*, external duplicature of the pallial edge; *pa''*, internal ditto; *pa'''*, median ditto; *su'*, *su''*, first and second sutures of the pallial edges. (After Deshayes.)

The edges of the two pallial lobes may remain free throughout their extent; this is the case in *Nucula*, the Anomiidae, the Arcidae (Fig. 188) the Trigoniidae, and the Pectinidae (Fig. 235). In all other Lamellibranchia the pallial lobes are partially united by the concrescence of the internal reduplicature of their margins; this union may be localised in one, two, or even three more or less extensive regions. Thus, there is only one line of union in the Solenomyidae (in which it is long, Fig. 231), the Aviculidae, the Ostraeidae, *Entovalva*, *Scioberetia*, the Mytilidae, the Carditidae, the Astartidae, the Crassatellidae, the majority of the Lucinidae, the Unionidae (Fig. 242), and in certain species of Cyrenidae; in other words, in a very large number of Submytilacea. This single line of union is always posterior, and is the prime factor in the formation of an aperture opposite to the anus (Fig. 231, *a.or*) known as the exhalant pallial or "anal" orifice. It serves for the evacuation of the excrements, of the water which has been used for respiration, etc., and is, in the manner indicated, entirely cut off from the rest of the pallial aperture through which the respiratory and food-bearing currents of water find an entrance, and through which the foot is thrust out. Lamellibranchs with this disposition of the pallial border have received the name of "Bifora." It should be noted that

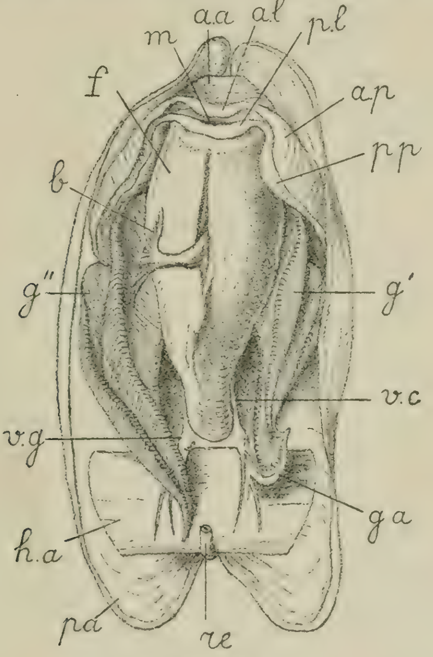

Fig. 188.

Arca lactea, Linnaeus, ventral aspect. *a.a*, anterior adductor; *a.l*, anterior lip; *a.p*, anterior labial palp; *b*, byssus; *f*, foot; *g′*, internal gill-plate; *g″*, external gill-plate; *g.a*, gill-axis; *h.a*, posterior adductor; *m*, mouth; *pa*, mantle; *p.l*, posterior lip; *re*, rectum; *v.c*, visceral commissure; *v.g*, visceral ganglion. (After Deshayes.)

in many Unionidae the anal orifice is itself divided into two, the more anterior aperture being dorsal and the more posterior—considered topographically—being the anal opening proper. In addition to the first fusion, there is a second in the Ledidae among the Protobranchia, in the Dreissensiidae and the Mutelidae among the Submytilacea, and in all other Eulamellibranchia and the Septibranchia (Fig. 249). In *Castalia*, a member of the Mutelidae, it has been observed that the second fusion may be present or absent in different individuals. This second fusion of the pallial borders is always pretty close to the first (Fig. 241), and forms the boundary of an orifice almost in juxtaposition to the anal aperture, leaving in front a third orifice (Fig. 241, *o.p*): hence the name "Trifora" given to Lamellibranchia which exhibit this arrangement. The second orifice is called the branchial or inhalant, and the third the pedal orifice. The last-named is generally very large (Figs. 194, 221, *o.p*, etc.), but its extent is always in inverse ratio to the extent of the second fusion and in direct ratio to the size of the foot protruded through it (Figs. 219, 246). In the genus *Kellya*, however, it is not the third or anterior aperture that serves for the passage of the foot, but the second or ventral aperture (Fig. 187, *o″*). Finally, when the second fusion extends for a long distance, that is to say, when the foot is very anterior, rudimentary, or cylindrical, a fourth pallial aperture may be formed between the pedal and branchial apertures, and therefore within the region of the second fusion. This disposition may be seen in some Solenidae, in *Lutraria* and *Glycimeris*, and in sundry Anatinacea, such as *Myochama*, *Chamostraea*, *Thracia*, *Pholadomya*, and *Aspergillum*, which are sometimes called, on this account, "Quadrifora." This fourth orifice probably arises as a subdivision of the pedal orifice; it is placed far forward in *Solen*, and is both inhalant and

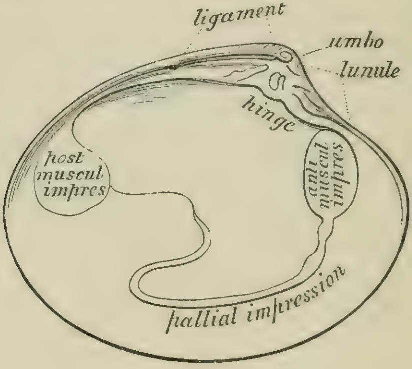

FIG. 189.

Left valve of *Meretrix*, from the inner face. (From Lankester, after Owen.)

exhalant in this genus; but is posterior and only exhalant in *Lutraria*, *Thracia*, etc.

Frequently the two posterior pallial orifices, anal and branchial, or at least the anal, as in some Lucinidae, are more or less prolonged in the form of muscular tubes which may be extended for a greater or less distance beyond the shell (Fig. 190); this feature is found in the majority of burrowing and boring Lamellibranchs. These tubes are known as siphons, and may be either—(1) independent of one another throughout their length, as, for example, in the Tellinidae (Figs. 190, *br.s*, *a.s*; 245, *g*, *g′*), Donacidae, *Thracia*, etc.; or (2) partially fused together, as may be seen in *Tapes*, *Solenocurtus* (Fig. 194), *Saxicava* (Fig. 246); or (3) completely united to one another, as in *Mactra*, *Dosinia*, *Mya*. *Lutraria*, *Pholas*, *Teredo* (Fig. 195), etc. The branchial siphon is usually the longer of the two, and in *Scrobicularia* is more than four times as long as the body. Sometimes the siphons may attain to a still greater degree of development, and may form an important part of the body-mass, or even surpass it in size. The extreme limit of evolution in this direction is exhibited by *Teredo*, in which these organs, while receiving the same nerve supply as in other Lamellibranchia, constitute the greater part of the mass of the animal; the anal siphon extends right forward and the branchial siphon contains the gills, as is also the case in *Solenocurtus*, *Fistulana*, *Saxicava*, etc.

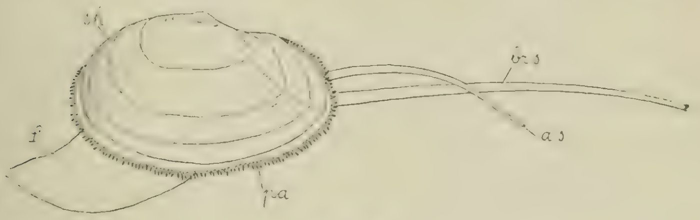

FIG. 190.

Tellina planata, left-side view. *a.s*, anal siphon; *br.s*, branchial siphon; *f*, foot; *pa*, tentaculiferous border of the mantle; *sh*, shell. (After Poli.)

There are two opposite currents in the pallial cavity. The first is postero-anterior in direction, and is set up by the action of the cilia clothing the surface of the branchiae; the second runs in the reverse direction on the ventral side near the edges of the mantle, and wards off foreign substances from the pallial cavity (*Mytilus*, *Cardium*, etc.). In *Pinna* and *Solen* this second current is created by a large longitudinal ciliated ridge on each side.

The two lobes of the mantle are furnished with several distinct pallial muscles which are inserted on the shell and are divisible into the following distinct groups:—(1) The orbicular muscle, extending right round the periphery of each lobe, and serving to attach it to the shell and as a retractor of the pallial border. (2) At the posterior end a specialised part of the orbicular muscle originates from and serves as the retractor of the siphons (Fig. 191, *m.s*); its development is proportional to that of the siphons, and it interrupts the evenly curved line formed by the orbicular muscle. The muscles leave an "impression" on the inner surface of each valve of the shell, and the impression of the orbicular muscle or "pallial impression" (Fig. 189) is indented by a "sinus" formed by the siphonal muscles. This "sinus" is scarcely ever absent in siphonate forms except in the Lucinidae and in *Cuspidaria*, in which the siphons are not retractile, and in the latter genus are protected by prolongations of the posterior part of the shell. (3) The adductor muscles of the shell are transverse pallial muscles uniting the two lobes of the mantle and the two shell-valves secreted by them. There are at the most two adductors; the anterior is dorsal and in front of the buccal aperture (Figs. 188, *a.a*; 191, *m.a*), but extends considerably towards the ventral side in *Modiolaria* and *Chama*. The anterior adductor muscle is the first to appear in development (*Nucula*, *Mytilus*, *Modiolaria*, *Pecten*, *Ostraea* (Fig. 192, A), *Dreissensia* (Fig. 224, *a.a*), Unionidae (Fig. 227, *i*), *Pisidium*, *Montacuta*, *Lasaea*, *Entovalva*, *Cardium*, *Pseudokellya*, etc.), but diminishes in importance

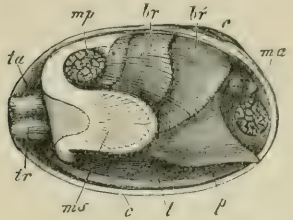

FIG. 191.

Right-side view of a *Mactra*, the right valve of the shell and right mantle-flap removed, and the siphons retracted. *br*, *br'*, outer and inner gill-plates; *c*, umbo of the shell; *m.a*, anterior adductor muscle; *m.p*, posterior adductor muscle; *m.s*, pallial retractor muscle of the siphons; *p*, foot; *t*, labial palp; *ta*, anal siphon; *tr*, branchial siphon. (From Lankester, after Gegenbaur.)

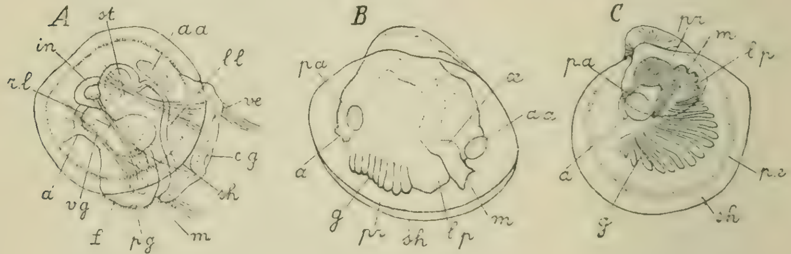

FIG. 192.

Three stages in the development of *Ostraea*, right-side view. *A*, protomonomyarian stage of *O. edulis* (after Woodward); *B*, dimyarian stage; and *C*, deutomonomyarian stage of *O. virginiana* (after Jackson). *a*, anus; *a.a*, anterior adductor; *c.g*, cerebral ganglion; *f*, foot; *g*, gill; *in*, intestine; *l.l*, left liver; *l.p*, labial palp; *m*, mouth; *oe*, oesophagus; *p.a*, posterior adductor; *p.e*, pallial edge; *p.g*, pedal ganglion; *pr*, prodissoconch; *r.l*, right-liver lobe; *sh*, shell; *st*, stomach; *ve*, velum; *v.g*, visceral ganglion.

in adult Mytilidae, and disappears altogether in *Mytilus latus* (Fig. 193, E) and *M. meridionalis*. It is very small or more usually absent in the Anomiidae, the Pectinacea, and the Ostraeacea, much reduced in *Teredo*, and absent in the adults of *Philobrya*, *Mülleria*, and *Tridacna*.

The posterior adductor muscle is ventral and anterior to the anus (Figs. 188, *h.a*; 192, C, *p.a*). When the anterior adductor is diminished in size or disappears in the adult, the posterior adductor necessarily becomes more central in order that its mechanical efficiency may be increased. This may be seen in the forms known as Monomyaria, and is accompanied by a shortening of the antero-posterior axis and a proportional increase of the dorso-ventral axis of the body, a phenomenon particularly well marked in the Tridacnidae. It should be observed that the species with a single adductor muscle belong to very various groups and are generally sessile forms: the Monomyaria, therefore, are polyphyletic and do not constitute a natural group. A single family may contain examples of Isomyaria, Anisomyaria, and Monomyaria (Fig. 193, C, D, E), and all, in the course of their development, pass through three different stages with regard to the arrangement of the adductor muscles. In the first stage, called the protomonomyarian stage, the anterior adductor, being the first to be formed, is alone present. In the second stage the two adductors coexist; this is the dimyarian

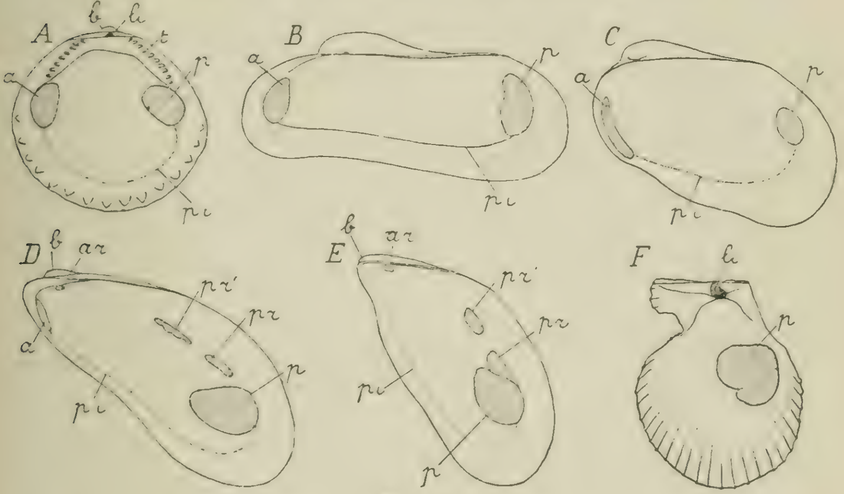

Fig. 193.

Right valve of six various Lamellibranchs, showing the various stages of the morphological development of the adductor muscles. *A*, *Pectunculus*; *B*, *Myrina*; *C*, *Modiolaria*; *D*, *Modiola*; *E*, *Mytilus latus*; *F*, *Pecten*. *a*, anterior adductor; *a.r*, anterior foot retractor; *b*, shell beak; *li*, ligament; *p*, posterior adductor; *p.i*, pallial impression; *p.r*, *p.r'*, posterior retractors of foot and byssus; *t*, hinge-tooth.

stage (Fig. 192, B). In the third or deutomonomyarian stage, the anterior adductor has disappeared (Fig. 192, C).

The two adductors, by their contraction, bring together the valves and close the shell. They are diminished in size when the valves lose their mobility, as, for example, in *Galeomma*, *Ephippodonta*, and *Scioberetia*, and they actually disappear in *Aspergillum* and *Chlamydoconcha*. These muscles are generally perpendicular to the surfaces of the valves, but in some Lamellibranchia that are fixed by one side, they may be very oblique, *e.g.* *Anomia*, *Pecten*, the Rudistae. The fibres of the adductors are attached to epithelial cells of the mantle which produce the hypostracum or substance of the muscular impressions. In many cases the fibres of each adductor may be divided into two distinct parts of different appearance (*Pecten*, *Ostraea*, etc.), of which the principal part in the monomyarian Lamellibranchs is formed of apparently striated fibres (see p. 5), this apparent striation being particularly well defined in the muscles of the swimming Lamellibranchs, Pectinidae, and Limidae, which are capable of very rapid contraction. The absolute force exerted by the adductor muscles is analogous to that of vertebrate muscles: in some cases they can resist the traction of a weight equal to several thousand times the weight of the animal deprived of its shell.

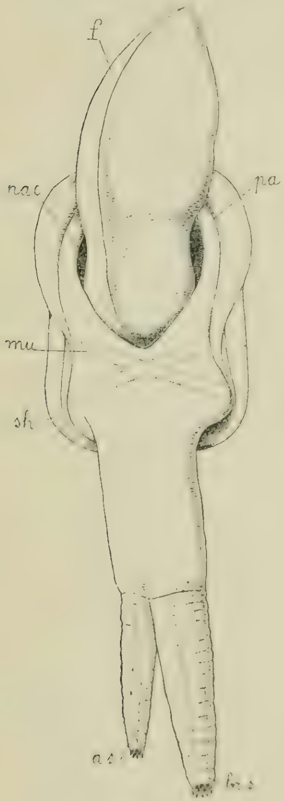

FIG. 194.

Solenocurtus strigillatus, ventral aspect. *a.s*, anal siphon; *br.s*, branchial siphon; *f*, foot; *mu*, cruciform pallial muscles; *pa*, mantle; *pa.c*, pallial cavity; *sh*, shell. (After Pelseneer.)

In the siphonate Lamellibranchia the pallial fusions separating the branchial and pedal orifices are often furnished with crossed muscular bundles, called cruciform muscles, passing from the edge of one valve to that of the other, and thus forming accessory adductor strands: these may be seen in *Tellina*, *Syndosmya*, and *Donax* among the Tellinacea, and in *Solenocurtus* (Fig. 194, *mu*). In species called "closed," in which the mantle fusions are very extensive, these muscles are continuous along the whole ventral border of the valves, between the pedal and branchial orifices (*Saxicava*, Fig. 246, *pa*).

The shell of Lamellibranchs is formed of two valves, each corresponding to a lobe of the mantle. The internal layer of the shell is secreted by the whole external surface of the mantle, but the external layer is secreted only by the thickened mantle edges. The internal layer is often nacreous, and may exhibit pathological products called "pearls," which are formed by the secretion of nacreous substance by the mantle round foreign bodies. These are generally of parasitic origin: the scolex of a Cestode forms the nucleus of a pearl in the genus *Meleagrina* of Ceylon and the Gambier islands; the larvae of Trematodes form similar nuclei in various European Lamellibranchs.

Though they are primitively symmetrical and commonly remain so, the valves become very asymmetrical in some species of *Arca*, in the Anomiidae, *Pecten*, *Ostraea*, *Corbula*, *Chama*, *Pandora*, *Myochama*, the Rudistae (Fig. 244), etc. In certain somewhat modified forms in which the foot, though more or less large, is feebly retractile, the valves do not meet and fit perfectly together along the ventral edge and are "gaping," as may be seen in the Pholadidae, Gastrochaenidae, etc. But with the exception of *Chlamydoconcha* and *Scioberetia*, in which the shell is internal, the valves fit together perfectly along the dorsal border, and are articulated with one another by a system of teeth and sockets which collectively form the hinge (Fig. 189), and only tend to be atrophied in forms whose valves have little mobility, especially in boring species. The valves are additionally united (except in the Pholadidae and Teredinidae, hence named Adesmacea, and a few other forms) by a ligament of a chitinous nature. This ligament is primitively continuous with the shell, and is, in fact, the uncalcified portion of the pallial cuticle, that is to say, of the originally single shell. The ligament finally becomes external (Fig. 189) or internal; in the latter case it is a "resilium." Its action is antagonistic to the adductor muscles, and consequently it causes the valves of the shell to gape.

In the youngest stages of the Protobranchia, Filibranchia, and various Eulamellibranchia, a series of little transverse denticulations, constituting a primitive hinge or provinculum (Bernard), is developed on each side of the ligament, or at any rate behind it in forms devoid of an anterior adductor muscle. The permanent hinge teeth are only formed at a later period, by the growth of distinct laminae on the surface of the hinge. Thus, in the typical Eulamellibranchia, the first lamellae originate at the extremities of the hinge surface, below the provinculum, and grow towards the centre of the hinge area; the internal ends of the anterior lamellae become hook-shaped, and their hooks become separated from their external ends; the latter form the anterior lateral teeth, while the hooks become the cardinal teeth, and the posterior lamellae give rise to the posterior lateral teeth.

Sundry methods have been proposed for representing the hinges of Lamellibranchs by formulae. The most logical is that of Munier-Chalmas and Bernard, which takes the origin of each element into account. In this system the primitive lamellae are indicated by Roman numerals, even numbers being used for the left valve, odd numbers for the right valve, preceded by the letter A if they are anterior to the ligament, by the letter P if they are posterior to it. Each definitive tooth is indicated by an Arabic numeral corresponding to the number of the primitive lamella from which it is derived (A2 in the case of AII, etc.), and is preceded by the letter C if it is a cardinal, or L if it is a lateral tooth, and is further followed by the letters *a*, *b*, etc., if it corresponds to the first, second, or other segment formed by the folds of the lamella. Thus CA2*b* stands for the left cardinal tooth originating from the posterior segment of the anterior lamella II.

In some exceptional cases the two valves of the shell are fused together dorsally; such shells are called symphinote, and examples may be found in the adults of some species of *Pinna*, *Unio*, *Anodonta*, and *Hyria*. But even when the borders of the mantle are almost completely fused together on the ventral side, the two valves are never fused ventrally to form a single tube like the shell of the Scaphopoda. Nevertheless, when the shell gapes and the mantle borders are largely fused together and provided with long conjoint siphons, the portions of the mantle that project beyond the valves may secrete a long calcareous tube (*Teredo*, *Fistulana*), which may be fused to the shell, as in *Aspergillum*, or the two valves themselves may be fused together dorsally as in the four genera mentioned above. In some other siphonate Lamellibranchs with gaping shells the portions of the mantle that project from the shell may secrete accessory protective sclerites, which may be independent of the valves, as, *e.g.*, the dorsal sclerites of *Pholas* and the sclerites of certain species of *Thracia*, or may be united to the shell as is the siphonal tube of *Pholadidea*. In *Teredo* two movable calcareous plates, actuated by special muscles, are formed symmetrically right

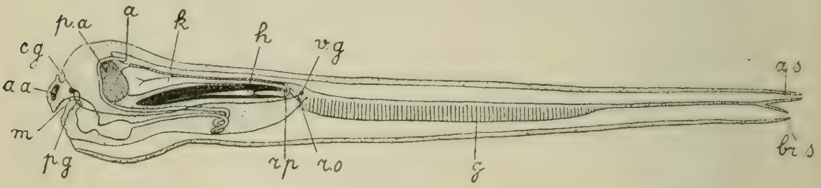

FIG. 195.

Sagittal median section of *Teredo*. *a*, anus; *a.a*, anterior adductor muscle; *a.s*, anal siphon; *br.s*, branchial siphon; *c.g*, cerebral ganglion; *g*, gill; *h*, heart; *m*, mouth; *p.a*, posterior adductor; *p.g*, pedal ganglion; *r.o*, renal opening; *r.p*, reno-pericardial orifice; *v.g*, visceral ganglion. (Partly after Grobben and Beuck.)

and left of the free extremity of the siphonal mass. These "pallets," as they are called (Fig. 247, II), probably serve to protect the free extremities of the siphons.

The valves generally bear on their internal surfaces distinct impressions of the insertions of the pallial, orbicular, siphonal adductor and retractor muscles of the foot, and therefore it is possible to infer something of the organisation of the animal in the case of fossil species. In general, the anterior side of the shell of the Lamellibranchia is the shorter, and the "umbones" or summits of the two valves are directed anteriorly, but in some forms, called for this reason "opisthogyrous," the posterior side is the shorter: such are *Nucula, Donax, Montacuta, Entovalva*, and *Cyrtodaria.*

The larval portion of the shell, or "prodissoconch," like that of the Gastropoda, is often distinct from the following portion, and may even be separated from it by a crest or ridge (Fig. 196, *p*): this feature is especially well marked in incubatory forms with large embryos. Also, in the same manner as has been described for Gastropods, the external duplicature of the mantle border may be reflected over the outer surface of, and cover a more or less considerable extent of, the shell in the Galeommidae and in the endoparasite *Entovalva* (= *Synapticola*). By an exaggeration of this process the mantle may even come to form a closed sac around each valve, a feature which may be seen in the three genera *Ephippodonta*, *Chlamydoconcha*, and *Scioberetia*, and also in a species commensal with a Synapta in the Philippines (Semper).

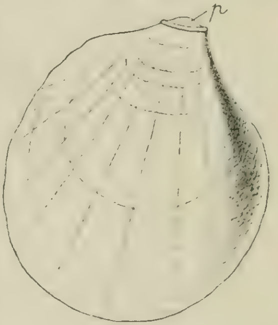

Fig. 196.
Philobrya sublaevis, right valve, outer aspect. *p*, prodissoconch.

As in the other classes of the Mollusca, the foot is a muscular projection from the ventral surface; its size and form are very variable, according to the habit of life adopted by the animal. The mass of the foot is frequently invaded by a portion of the viscera, at least by a part of the digestive canal, the liver, and the gonads, the last-named being superficial. In species in which the foot is very mobile, its two lateral faces are united by transverse muscular bundles.

In its most primitive form the foot is a cylinder, more or less flattened from side to side, and terminated by a ventral plantar surface (Protobranchia, Figs. 230, 231; *Pectunculus*, *Modiolarca*, Fig. 241). But more usually the foot is still further flattened, and terminates below in a more or less elongated keel, which may end in two points, an anterior and a posterior as in *Trigonia*, or in a single point, which is always anterior. This latter arrangement is the most common, and is found, for example, in the Unionidae (Fig. 242), *Tellina* (Fig. 190, *f*), and *Cardium* (Fig. 243). The anterior pointed end may be so much elongated, for example, in *Poromya*, as to give the foot the appearance of a cylindrical tentacle, sometimes slightly swollen at its free extremity (many Lucinidae, Fig. 238, III), or of a long cylinder directed forward and sometimes ending in a swelling of constant shape (*Solen*, *Mycetopus*). In some cases the foot may secondarily acquire an enlarged free extremity with a creeping surface, *e.g.* in *Galeomma*, *Lepton*, and certain species of *Erycina*. In *Spondylus* it ends in a pedunculated globular appendage. Some Anatinacea, such as *Pholadomya* and *Halicardia*, have an accessory foot-like organ, the so-called opisthopodium, on the posterior extremity of the visceral mass. In *Mytilus*, also, a distinct posterior carinated projection may be seen behind the extensible pedal cylinder; this has been called the "Punch's hump." There is, on the other hand, an anterior and dorsal tongue-shaped projection on the foot of *Tapes decussatus*.

Finally, the foot may become rudimentary through disuse in genera with restricted or no locomotory powers. This is especially the case in boring Lamellibranchs with extensive fusion of the mantle edges, such as *Pholas* and *Teredo* (Fig. 247, VI), and in such forms as are fixed by a byssus or by the substance of the shell, such as *Pecten* (Fig. 235, *f*), *Ostraea*, *Aetheria*, etc.

The foot, then, is the locomotory organ, as it is in other Mollusca. Its special function is to grope in the shifting soil and to slowly drag along the animal by its successive contractions and extensions, its anterior extremity being supported or fixed. These movements of the foot are due to turgescence, produced by the afflux of blood into the pedal sinuses, and its subsequent contraction by means of the retractor muscles.

The foot is never provided with an aquiferous pore through which, as was for a long time believed, water can penetrate into the circulatory system. But it very frequently presents a more or less posterior orifice in the middle line corresponding to the ventral pedal pore of Gastropoda (Fig. 144, I) and leading into a cavity known as the byssogenous cavity (Fig. 197, I), into which certain unicellular glands situated in the foot discharge their secretion. This secretion, passing between the epithelial cells of the byssogenous cavity, hardens on contact with the water and forms threads of conchiolin, which unite to form the trunk of the byssus (Fig. 197, IV). This structure serves to attach the animal, but the fixation is not necessarily permanent; the old byssus may be abandoned and a new one formed (*Arca*, *Mytilus*, *Avicula*, *Dreissensia*, etc.). The byssogenous organ is poorly developed in the Protobranchia, in which group the byssogenous cavity is situated far back (Fig. 204, VIII), and a functional byssus is absent. When it attains to its maximum of specialisation the byssogenous cavity presents a number of internal folds or plates (Fig. 197) which increase the secreting surface; the trunk of the byssus is thick (Fig. 199, IV), is formed more or less deep in the mass of the foot, and becomes engaged in a semi-cylindrical groove hollowed out along the ventral keel of the foot in front of the orifice of the byssogenous cavity (Fig. 236, *b.gr*). The walls of this groove contain a considerable number of large unicellular mucous glands. The byssus is particularly well developed in *Anomia*, *Arca* (Figs. 188, 199), *Mytilus*, *Pinna*, *Avicula* (Fig. 236), *Pecten*, various Myacea (*Saxicava*, etc.), Anatinacea (*Lyonsia*), Cardiacea (*Tridacna*), *Dreissensia*, etc. In the genus *Anomia* the byssus is of peculiar form, being partly calcified and of a

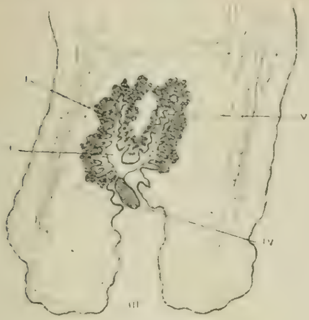

FIG. 197.

Transversal section of the foot of *Lyonsia*, through the byssus-orifice. I, byssogenous glands; II, byssus-cavity; III, byssus-orifice of the foot; IV, byssus; V, roots of the byssus.

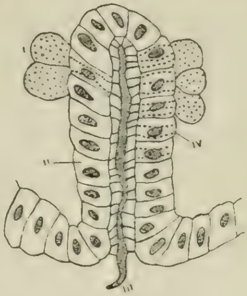

FIG. 198.

Transversal section of a groove of the byssogenous cavity of *Modiolaria discors*. I, byssogenous glands; II, epithelium of the byssogenous cavity; III, roots of the byssus; IV, secretion of the byssogenous glands passing between the epithelial cells. (After Cattie.)

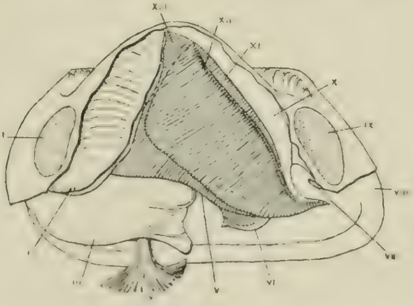

FIG. 199.

Arca lactea, Linnaeus, left-side view (the left half of the mantle removed). I, anterior adductor; II, labial palps; III, foot; IV, byssus; V, ventral edge of the internal left gill-plate; VI, right gill; VII, anus; VIII, mantle; IX, posterior adductor; X, branchial axis; XI, direct lamina of the external gill-plate; XII, reflected lamina of the external gill-plate. (After Deshayes.)

stony consistence, whence it is called the "ossiculum"; it projects on the right side through a hole in the flattened valve of that side.

In *Modiolarca* the byssogenous cavity is preceded by a second glandular cavity (Fig. 241, *gl.p*), but the latter takes no part in the secretion of the byssus. In some cases the whole of the byssogenous cavity degenerates in the adult, as may be seen in certain species of *Unio*, or it is closed as in *Cyclas*, in which genus it and the byssus are highly developed during embryonic life. In the endoparasite *Entovalva* the byssogenous apparatus appears to be modified to form a so-called "organ of adhesion" (Fig. 240, *f.gl*).

The foot, with the viscera contained in it, is attached to the shell by retractor muscles, of which there are normally four pairs. Two pairs, the retractors and protractors, are anterior and situated near the anterior adductor muscle; one pair, the elevators, is median; and one pair of retractors is posterior and close to the posterior adductor muscle. These various muscles are inserted symmetrically near the dorsal border of the valves and between the two adductors. In the more primitive Lamellibranchs these muscles are greatly extended in a longitudinal direction (Fig. 231, *f.e*), and in certain Protobranchia they may form an almost continuous series; but otherwise it is only the four retractors at the extremities of the foot that are well developed, the remainder being rudimentary or atrophied (Fig. 202, *a.f.r*, *p.f.r*). In general, the so-called Monomyaria, or forms with a single and that the posterior adductor, have only retained the posterior retractors of the foot, and these muscles only exist on one side in various forms that are fixed by one valve: thus in *Pecten* only the left retractor is present, and even this is aborted in *P. magellanicus*. When the foot becomes reduced as an organ of locomotion, and, in compensation, the byssogenous apparatus assumes a large size, the retractor muscles, especially the posterior pair, take their origin from the latter structure, and thus become the retractor muscles of the byssus.

II. ANATOMY.

1. *The Alimentary Canal.*—The mouth is situated at the anterior end of the body, dorsal of the base of the foot (Fig. 188, *m*). In *Solenomya* (Fig. 231, *m*) it lies behind the anterior adductor muscle, but it is on the ventral side of this muscle in all other Lamellibranchia with two adductors. Except in *Anomia*, in which it is asymmetrical, it is a symmetrical transverse aperture compressed between two lips, of which one is dorsal and anterior, the other is ventral and posterior. These lips have simple borders as a rule, but in the Pectinidae they are scolloped and even ramified (Fig. 235, *l*); they are generally continued on either side into two lobate prolongations, called the labial palps, of which the external is the prolongation of the anterior lip. In the genus *Arca* (Fig. 188) the lips pass insensibly into the

palps, but usually the palps become suddenly much broader than the lips. The palps are formed from part of the velar area of the larva and assume various forms, but are most commonly triangular. Their inner surfaces are transversely folded and ciliated in such a manner as to conduct all particles coming within their reach into the buccal orifice. They are poorly developed or absent in various Lucinidae, such as *Axinus* (Fig. 238) and *Corbis*, and in *Limopsis* and some species of *Cuspidaria*. On the other hand, they are very large in the Tellinidae, surpassing the gills in size in this family, and the anterior pair is very large in *Poromya* (Fig. 249, *a.p*). In the Nuculidae and Ledidae the posterior angles of each pair of palps are produced to form a common tentaculiform appendage bearing a groove along the whole of its ventral surface; these appendages can be thrust out beyond the shell and assist in obtaining food (Fig. 200, *p.ap*). In *Solenomya* the two palps are rudimentary, but the tentacular prolongation persists in the form common to the other Protobranchia, with its ventral groove forming a continuation of the interlabial space (Fig. 231, *p.l.*).

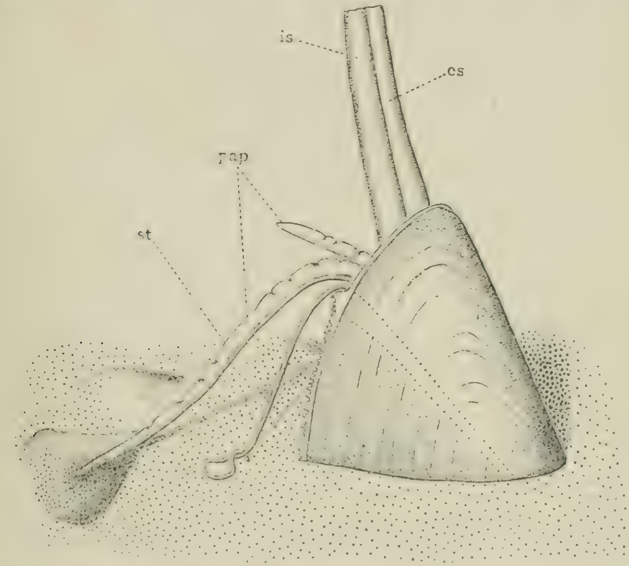

Fig. 200.

An adult specimen of *Yoldia limatula*, as it appears while feeding—partially immerged in mud. *c.s*, exhalant siphon; *i.s*, inhalant siphon; *p.ap*, palp appendages; *s.t*, siphonal tentacle. (After Drew.)

In the family Nuculidae among the Protobranchia there is still an anterior dilatation of the alimentary canal representing the buccal cavity and provided with two lateral and symmetrical glandular pouches; but in all other Lamellibranchia the mouth leads directly into the stomach through a short oesophagus (Fig. 201, *oe*), which is rarely muscular (*Poromya*) and is sometimes nearly aborted. The stomach is a large and generally laterally compressed ovoid or piriform sac, more or less deeply buried in the viscero-pedal mass (Figs. 207, *st*; 231 and 234, *st*). Its walls are thin and not muscular except in some carnivorous forms such as the Septibranchia. The stomachal epithelium is lined with a thick but caducous cuticular coat, visible even in the larval stage (*Ostraea*, Fig. 192, A): this cuticle serves to protect the secretory cells of the stomach.

The stomach is very commonly provided with a pyloric caecum, lined by a richly ciliated columnar epithelium. The caecum may be long, especially in *Donax*, *Mactra*, *Solen*, *Pholas*, and *Teredo*, and sometimes extends into the ventral part of the foot, or into the mantle, penetrating into the right lobe in *Anomia*, the left lobe in *Mytilus latus*. It is, however, short in some forms, *e.g.* in *Trigonia*. It corresponds to the caecum of the crystalline style in certain Gastropoda (*Pterocerus*, Fig. 75), and like it contains a cylindrical product, the crystalline style (Fig. 201, *cr.s*), which is more or less continuous with the cuticular lining of the stomach. In the following forms the caecum is fused with the initial part of the intestine, and communicates with it by a narrow longitudinal slit: *Arca*, *Mytilus edulis*, *Ostraea*, *Pecten*, the Lucinidae (*Montacuta*), the Tellinidae and Psammobiidae, *Cardium*, the Unionidae, *Mya*, *Solenocurtus*, and the Septibranchia. The extremity of the crystalline style projects into the stomach and is gradually eroded by the action of the digestive secretions; the product of its solution forms a sort of cement which encrusts any hard substances that may have been ingested and thus protects the delicate walls of the intestine from injury. Sometimes the stomach is furnished with a second ventral caecum, which may be anterior, as in *Mytilus*, or posterior, as in the Pholadidae and Teredinidae (Fig. 195).

The liver consists of a pair of voluminous, more or less symmetrical acinous glands which occupy the whole space surrounding the stomach, and may extend into the foot (Figs. 207, 222, *hep*). Posteriorly and dorsally the liver is generally covered over by the gonads. In the adult Nuculidae and Ledidae the left lobe is the larger, and the coils of the intestine are situated on the right side. It should be noted that, in developmental stages, the left liver lobe of Lamellibranchia, like that of the Gastropoda, is larger than the right (Fig. 192, *l.l*, *r.l*). The hepatic orifices leading into the alimentary canal are often multiple, even in some Protobranchia, but in development and in many adult forms (*Solenomya*, *Adacnarca*, *Modiolaria*, various Erycinidae, *Pseudokellya*, etc.) there are only two more or less symmetrical orifices. As a result of specialisation these larval apertures may multiply, and various numbers are found in adult forms, viz. three in certain Nuculidae, in *Chama*, and *Spondylus*; four in *Arca*; five in *Pectunculus*, *Philobrya*, and *Pecten*; and as many as twelve in *Mytilus.* The lumen of the hepatic glands may be of considerable size, and form part of the digestive and absorptive cavity. In certain Lucinidae (*Montacuta*, *Axinus*, Fig. 238) the hepatic glands, together with the overlying gonads, project into the pallial cavity in the form of arborescent tufts.

The intestine almost always arises from the ventral side of the stomach, and is sometimes provided with a valve at its origin (*Pinna*). It is short and rectilinear or scarcely coiled in *Solenomya*, in sundry Filibranchia such as *Arca*, *Pectunculus*, *Limopsis*, *Philobrya* (Fig. 234), *Anomia*, and in the Septibranchia (Fig. 251, *in*); but more usually, as the Lammellibranchs are nearly all herbivorous, it describes a certain number of convolutions in the viscero-pedal mass (Fig. 242, *al*). These may vary from one to a dozen in number, and sometimes they are confined to one side of the body; in the Nuculidae and Ledidae, for example, they are on the right side. The intestine is ciliated throughout its whole length, and its rectal portion is generally provided with an internal longitudinal ridge. In *Nucula* (Fig. 204, XIV), *Arca*, and *Anomia* the rectum passes ventrad of the ventricle of the heart, as it does in Amphineura; but it traverses the ventricle, in rhipidoglossate fashion, in the majority of Lammellibranchia. But in *Malletia*, *Avicula*, most species of *Ostraea*, *Mülleria*, and *Teredo* (Fig. 195) it is dorsad of the heart. Finally, the rectum always passes over the dorsal side of the posterior adductor muscle, and ends behind it in

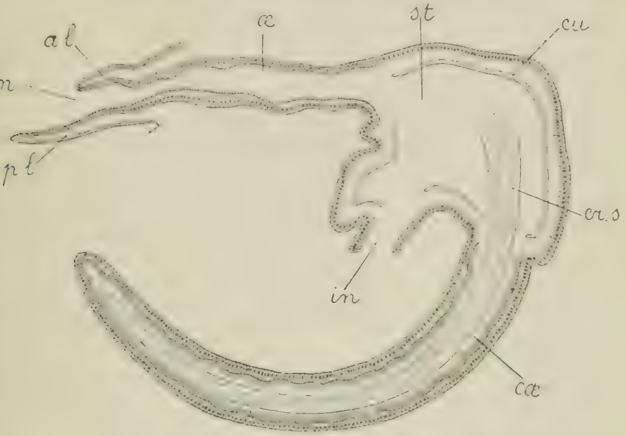

Fig. 201.

Median sagittal section of the anterior part of the digestive tract of *Donax.* *a.l*, anterior lip; *cae*, caecum; *cr.s*, crystalline style; *cu*, stomachal cuticle; *in*, intestine; *m*, mouth; *oe*, oesophagus; *p.l*, posterior lip; *st*, stomach. (After Barrois.)

the middle line, except in a few fixed forms, such as *Pecten* (in which the anus is to the left of the middle line, Fig. 234, *a*), *Ostraea*, etc. In some species of *Pecten* and *Lima* the rectum is recurrent, and nearly completely surrounds the posterior adductor muscle. In some special cases, viz. in various Aviculidae, and especially in *Pinna*, the free extremity of the rectum bears an erectile appendage.

2. *Circulatory Apparatus.*—The vascular system of Lamellibranchs, like that of all other Molluscs, is completely closed, and water cannot possibly enter into the circulation. The system is composed of more or less dilated and spacious, but none the less true vessels, and of sinuses with connective tissue walls, but without an endothelium. Not only is the vascular system completely cut off from the surrounding medium, but it is also cut off from the pericardial cavity, as may clearly be seen in red-blooded forms, whose pericardial fluid is colourless and, like that of other Lamellibranchs, totally devoid of blood corpuscles.

The blood always forms an important part of the mass of the body, often constituting a half of its weight. It contains nucleated amoeboid corpuscles (amoebocytes), and in some cases, particularly in arenicolous or limicolous species, non-amoeboid corpuscles containing haemoglobin. Such is the case in various species of *Arca* (*A. trapezia*, *A. pexata*, *A. tetragona*, etc.), in *Pectunculus violacescens*, *Tellina planata* (and around the nerve-centres in *T. fabula*), *Poromya granulata*, and some Solenidae such as *Ceratisolen legumen*. While red in these latter forms, the blood in certain Veneridae, Cardiidae, Dreissensiidae, etc., is of a bluish tint owing to the presence of haemocyanin. In addition to its normal function, the blood plays an important part in causing turgescence of tegumentary expansions, the mantle and siphons and the foot.

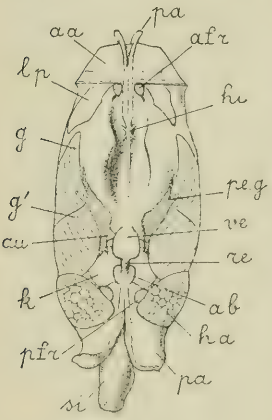

FIG. 202.

Tapes pullaster, without its shell, dorsal aspect, with several organs seen through the mantle. *a.a*, anterior adductor muscle; *a.b*, aortic bulb; *a.f.r*, anterior foot retractor; *au*, auricle; *g*, internal gill-plate; *g'*, exterior gill-plate; *h.a*, posterior adductor; *hi*, hinge-lobe of mantle; *k*, kidney; *l.p*, labial palp; *pa*, mantle; *pe.g*, pericardial gland; *p.f.r*, posterior foot retractor; *re*, rectum; *si*, siphon; *ve*, ventricle.

As in all other Mollusca, the central organ of the circulation is on the dorsal side (Fig. 202, *ve*), near the hinge of the shell, and is contained in a pericardium. In adult Anomiidae, however, it projects freely into the pallial cavity, behind the adductor muscle. The heart always consists of a median ventricle and two generally symmetrical auricles: it is only in such forms as *Anomia* that the auricles are altogether asymmetrical. The ventricle lies completely free in the pericardial cavity; it is, however, fused to the dorsal wall of the pericardium throughout its length in *Pliodon*, and for a part of its length in *Pandora*. The walls of the ventricle are always very muscular, and contain free and interlaced bundles or muscle fibres. The situation of the ventricle varies very much, even in tolerably closely related species: it is dorsad of the rectum in *Nucula* (Fig. 204), the Anomiidae, and *Arca*; traversed by the rectum in the great majority of Lamellibranchia (Fig. 231, *r*); and finally ventrad of the rectum in *Malletia*, *Ostraea* (except *O. cochlear*), *Mülleria*, and *Teredo* (Fig. 195). The ventral position of the ventricle, in species remotely allied to one another, is a phenomenon of convergence due to the shifting of the base of the gill away from the primitive position of the heart. It should be observed that the transition to the ventral position is to be seen in *Pinna*, *Perna*, and *Avicula*: in the first-named the ventricle still forms a very slender ring above the intestine, but in the two last genera it is simply attached for its whole length to the ventral side of the intestine. In *Nucula* and *Arca* the ventricle appears to be formed of two symmetrical halves: it is really elongated transversely, and contracted in the middle of its length. In adult Lamellibranchs the ventricle may beat rather slowly—*e.g.* twenty times per minute in the oyster, six times per minute in *Anodonta*—but in the young of *Ostraea* the pulsations may be as many as one hundred per minute.

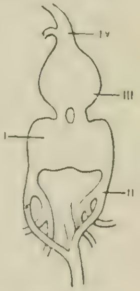

FIG. 203.

Heart of *Ostraea edulis*. I, the joined auricles; II, branchial efferent vessels; III, ventricle; IV, aorta. (After Poli.)

The auricles communicate with the ventricle by a narrow slit on each side, the apertures being provided with muscular valves which prevent the reflux of blood from the ventricle. The auricles are thick and muscular only in the Nuculidae, Solenomyidae, Anomiidae, and in a lesser degree in *Pectunculus*. In these diverse but relatively primitive forms (and also in *Pecten* and some other types), the auricle of either side is connected only with the anterior or basal extremity of the efferent branchial vessel, a disposition which is common to other groups of Mollusca and indicates the primitively posterior situation of the ctenidia. In this case the auricles are elongated (Fig. 204, XII) and their maximum diameter is close to the ventricle. In all other cases their walls are thin and moderately muscular, they enter into relation with the gills along a considerable extent of the efferent branchial vessel, and they are triangular in form (Fig. 234, *aur*), with the maximum diameter nearest the gill. When the ventricle contracts the auricles dilate, so that the three together always fill the pericardial cavity. The walls of the auricles are frequently invested with a brownish-coloured glandular epithelium, constituting the pericardial glands (see below, p. 233). Sometimes the two auricles communicate with one another inside the pericardium. In the Pectinacea (Pectinidae, Aviculidae) and Ostraeacea (Fig. 203), and also in *Pectunculus*, *Philobrya*, and the Mytilidae, this communication lies behind and to the ventral side of the ventricle and its aorta; in *Isocardia* it is anterior and dorsad of the aorta. The same tendency to the union of paired symmetrical organs may be seen in the kidneys and gonads.

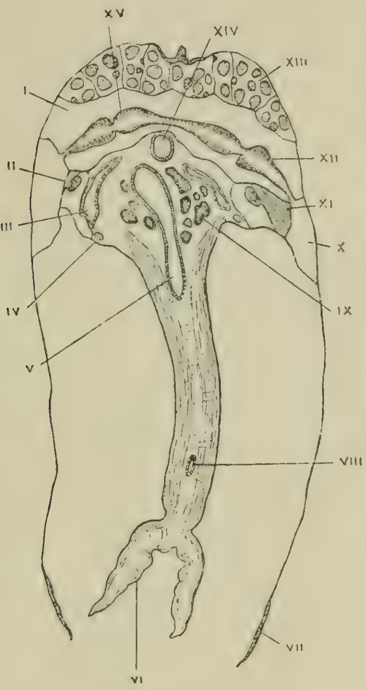

FIG. 204.

Nucula nucleus, transverse section through the heart. I, pericardium; II, genital duct; III, kidney; IV, visceral commissure; V, intestine; VI, foot; VII, mantle; VIII, byssus cavity; IX, liver; X, afferent sinus; XI, retractor muscle of the labial palps; XII, auricle; XIII, ovary; XIV, rectum; XV, ventricle.

When the circumanal complex — that is to say, the posterior adductor muscle, the mantle borders, and especially the siphons—are only slightly developed, the ventricle only gives off a single anterior aortic trunk, just as it does in the Amphineura and Gastropoda. This is the case in the Anomiidae and Mytilidae. Or the posterior aorta may be very small or indistinctly marked off from the anterior aorta, as in *Pectunculus* and some species of *Nucula*; but in all other Lamellibranchs, and especially in the siphonate forms, there are always two aortae, an anterior and a posterior, clearly separated from one another and of more or less equal importance. The anterior aorta is dorsad and the posterior ventrad of the intestine, except, of course, in *Nucula* and other forms in which the heart is dorsal. The pedal branch of the anterior aorta passes between the cerebral and pedal ganglion-pairs. In *Ostraea*, *Vulsella*, *Tridacna*, and *Teredo* the two aortae are secondarily fused to form one; again an instance of convergence in unrelated species, due to the shortening of the antero-posterior axis of the body.

The foot, the mantle, and the siphons derived from the latter are gorged with blood when their muscles are relaxed, and their sudden contraction often produces a reflux of arterial blood towards the heart. In Lamellibranchs with a well-developed foot and siphons, the return of blood into the ventricle is prevented by valves situated at the origins of the aortae, and a sphincter is also often to be found at the root of the posterior aorta, and sometimes a valve in the siphonal artery. In addition, highly developed aortic bulbs, separated from the ventricle by one of the above-mentioned valves, are frequently present, generally on the posterior aorta, where a large bulb may be seen, within the pericardium, in many Siphonates, particularly in the Veneridae (*Tapes*, Fig. 202, *a.b*), Petricolidae, Tridacnidae, Mactridae, etc. A bulb or aortic dilatation also occurs on the anterior aorta, inside the pericardium in *Pecten* and the Mytilidae, outside the pericardium in *Anodonta*. The arterial blood forced back towards the heart by the contraction of the foot or mantle or siphons enters and fills these various bulbs.

The blood carried to the different parts of the organism by the ultimate ramifications of the arterial trunks finally enters the venous sinuses, of which the most important are the pallial sinuses, the pedal sinus, and the great median ventral sinus. The last named is situated between the pericardium and the foot, and is separated from the pedal sinus by the valve of Keber, which prevents the foot from emptying itself of blood when in movement. It is from this great unpaired median sinus that the greater part of the blood is derived that passes through the kidneys and thence goes on to the gills. But a certain quantity of blood is carried to the auricles without having passed through the gills: this blood is brought from the mantle, for example, in *Pecten*.

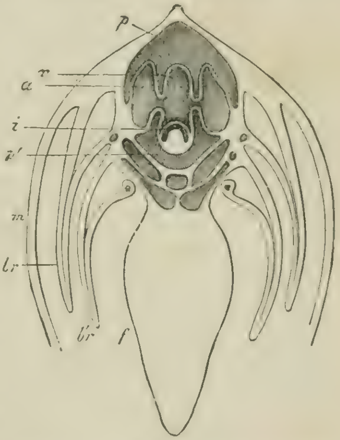

Fig. 205.

Transverse section through an *Anodonta*, about the mid-region of the foot. *a*, auricle; *br*, outer gill-plate; *b′r′*, inner gill-plate (each composed of two lamellae); *f*, foot; *i*, intestine; *m*, mantle-flap; *p*, *p′*, pericardial cavity. (From Lankester, after Gegenbaur.)

The essential respiratory organ of the Lamellibranchs is a pair of ctenidia. Each ctenidium is a lateral pallial offset, occupying a longer or shorter space between the mantle and the posterior part of the visceral mass. It may extend as far forward as the labial palps (Fig. 241, *br′*), but in the most archaic forms the gills still occupy a relatively posterior position (Figs. 230, 231, *g*), while in specialised forms they reach to the anterior extremity of the body (Fig. 221). Each ctenidium consists of a hollow vascular axis bearing on each face a row of more or less flattened hollow filaments, which are nothing more than simple expansions of the axis. In the Protobranchia the filaments are broad, simple, and free (Fig. 230, *g*), and the two rows are situated on opposite sides of the axis (Fig. 206, A, B). In all other Lamellibranchia the filaments are more or less narrow, and the two rows are normally parallel to one another and directed towards the ventral surface (Fig. 206, C–K). The distal moieties of the filaments are, however, reflected ectaxially and dorsalwards, in such a manner that each row forms a double lamina, that is to say, consists of two leaves or lamellae (Fig. 205, *br*, *br′*) between which there is an interlamellar space or cavity, serving, in some species, for the incubation of the ova.

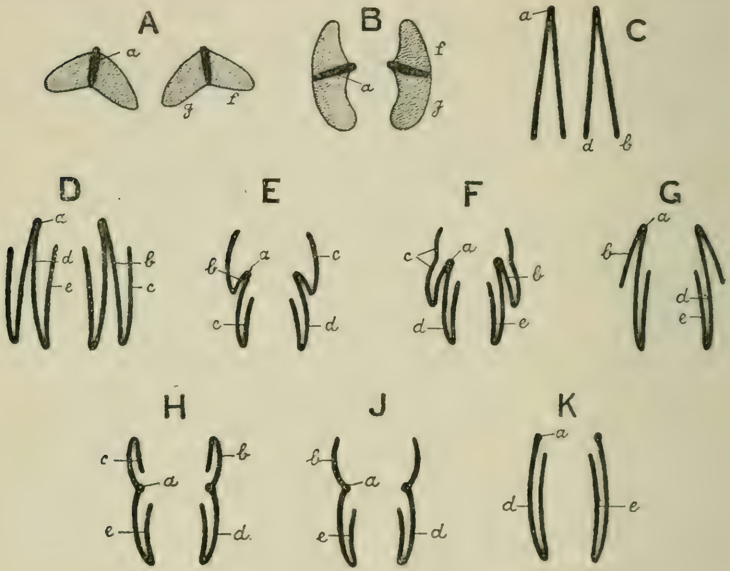

FIG. 206.

Diagrammatic sections taken transversely to the axes of the gills of various Lamellibranchs. *A*, *Nucula*; *B*, *Solenomya*; *C*, *Dimya*; *D*, the majority of the Lamellibranchs; *E*, *Donax faba*; *F*, *Donax variabilis*, *Tapes*, *Venus*; *G*, *Lasaea*; *H*, *Tellina*; *J*, *Lyonsia*; *K*, *Lucina*, *Montacuta*. *a*, axis; *b*, direct (usually descending) lamella of the outer gill-plate; *c*, reflected (usually ascending) lamella of the outer gill-plate; *d*, direct or descending lamella of the inner gill-plate; *e*, reflected or ascending lamella of the inner gill-plate; *f*, leaflets of the outer gill-plate; *g*, leaflets of the inner gill-plate. (After Ridewood.)

In the Filibranchia the successive filaments of each ctenidial row are locked together by ciliary junctions, sometimes specialised to form ciliated discs whose cilia interdigitate closely with one another (Fig. 210, A, *cj*). The direct and reflected limbs of each individual filament—and consequently the two lamellae of each gill-plate—are joined together by bridges or interlamellar junctions, which are formed of connective tissue only in the Pectinidae, but are vascular in the Aviculidae. Finally, the different elements of the branchial apparatus are much more intimately connected in the various groups of Eulamellibranchs, in which there are always vascular interfilamentar and interlamellar junctions (Fig. 237). Thus the blood brought to the gill by the afferent vessel is conducted by vessels which run between the lamellae and communicate with the filaments on either hand, forming in this manner the interlamellar junctions.

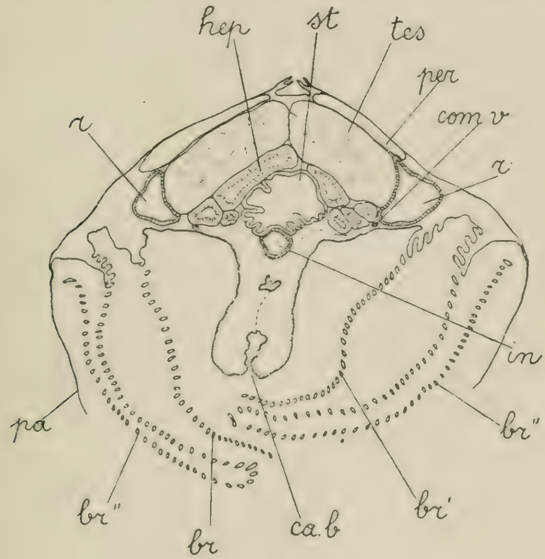

FIG. 207.

Adacnarca nitens, Pels., transverse section. *br*, right internal gill-plate; *br'*, left internal gill-plate (without reflected lamina): *br''*, external gill-plates (with reflected lamina); *ca.b*, byssus cavity; *com.v*, visceral commissure; *hep*, liver; *in*, intestine; *pa*, mantle; *per*, pericardium; *r*, kidney; *st*, stomach; *tcs*, testis.

Each gill-plate may be thrown into a very regular series of transverse folds, each fold involving a fixed number of filaments; this is the case in the Pectinacea, the Ostraeacea, and the more specialised forms of Eulamellibranchia. In the last-named the folding is still but slightly marked in the Veneridae, but becomes much more so in the Cardiacea (in *Tridacna* a single fold may contain as many as seventy filaments), the Myacea, etc. In the Pectinacea and Ostraeacea the filament forming the junction between two successive folds becomes thicker and more important than the others, constituting a principal filament lying at the bottom of the furrow between two successive folds. Not all the Lamellibranchia possess complete gills consisting of two gill-plates each formed of two reflected lamellae; in *Anomia aculeata* and *Dimya* none of the gill-plates have reflected lamellae; in *Adacnarca* the reflected lamella is absent from the inner plate (Fig. 207, *br′*); in *Lasaea* and all the Anatinacea there is no reflected lamella in the outer plate, and finally, the external plate is aborted in certain Lucinidae (*Lucina*, *Corbis*, *Montacuta*, *Cryptodon*), in *Scioberetia*, and the Teredinidae (Fig. 206, K). The external gill-plate, whether complete or not, instead of being directed ventrally with its lower border parallel to that of the inner plate, may be directed dorsally, and in such case may be without the reflected lamina, as in *Solenomya* (Fig. 231, *g*), or may possess it, and be either smooth, *e.g.* *Tellina* (Fig. 206, H), or folded, *e.g.* the Anatinacea.

The posterior, that is to say, the distal ends of the branchial axes are primitively free, as in the aspidobranch Gastropoda (Figs. 82, 127), and in such case the gills show no concrescence *inter se*, nor do the free extremities of the reflected lamellae unite with the mantle. This primitive condition is found in the Protobranchia (Fig. 231), the Arcidae (Fig. 208, *d*), the Trigoniidae, the Mytilidae, and the Pectinidae (Fig. 235, *g*); and among the Filibranchia it is only in the Anomiidae that the gills are united by the dorsal edges of the internal lamellae of the inner plates. But in all other Lamellibranchs the gills, in addition to this union, are joined to the mantle by the upper edges of the external lamellae of the outer gill-plate, and anteriorly, where the visceral mass interposes to prevent the union of the reflected lamellae of the inner gill-plates, these latter are attached to the viscero-pedal mass (Fig. 209, B, C, D). These various unions of the extremities of the reflected lamellae, whether with one another or with the mantle or with the viscero-pedal mass, may be effected by simple ciliary junctions—*e.g.* in *Avicula*, *Pinna*, *Anomia*, *Solen*, the Anatinacea—or by a true concrescence.

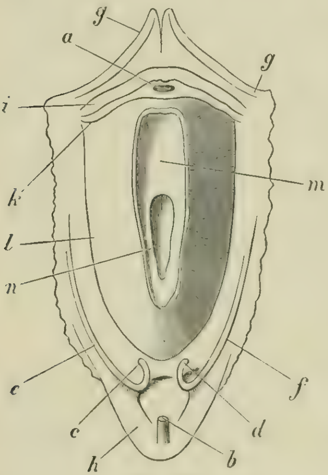

Fig. 208.

View of the ventral (pedal) aspect of the animal of *Arca noae*, the mantle-flap and gill-filaments having been cut away. *a*, mouth; *b*, anus; *c*, free curved extremity of the gill-axis of the right side; *d*, do. of the left side; *e*, *f*, anterior part of these axes fused by concrescence to the body-wall; *g*, anterior adductor muscle; *h*, posterior adductor muscle; *i*, anterior lip; *k*, posterior lip; *l*, base line of the foot; *m*, sole of the foot; *n*, byssus cavity. (After Lankester.)

The result of these multiple unions is that the gills form a partition, extending as far as the division between the two posterior, anal and branchial, pallial orifices (Fig. 209, D), and dividing the pallial cavity into two chambers, called respectively the supra-branchial or cloacal and the infra-branchial chamber (Fig. 209, *i*, *i*). The respiratory water generally enters the pallial cavity by the postero-ventral side (by the branchial orifice or by the branchial siphon, if the latter is differentiated); thence it passes, as through a filter, through the trellis-work of the branchial filaments constituting the partition in question, and is expelled from the supra-branchial chamber by the anal orifice of the mantle or by the anal siphon.

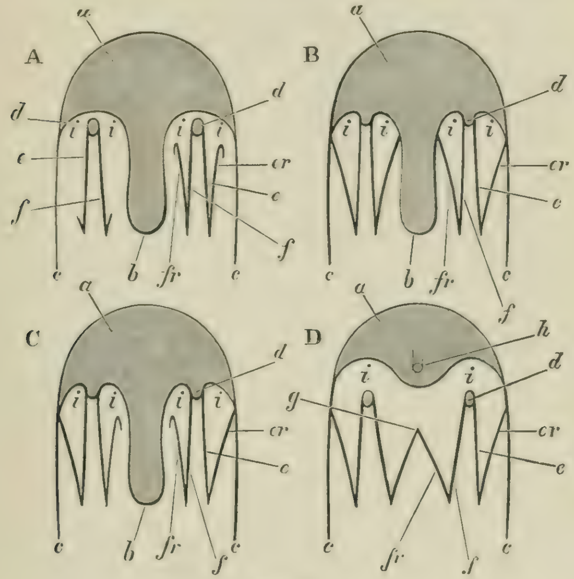

Fig. 209.

Diagrams of transverse sections of a Lamellibranch to show the adhesion, by concrescence, of the gill-lamellae to the mantle-flaps, to the foot, and to one another. *A* shows two conditions with free gill-axis; *B*, condition at foremost region in *Anodonta*; *C*, hind region of foot in *Anodonta*; *D*, region altogether posterior to the foot in *Anodonta*. *a*, visceral mass; *b*, foot; *c*, mantle-flap; *d*, axis of gill or ctenidium; *e*, adaxial lamella of outer gill-plate; *cr*, reflected lamella of outer gill-plate; *f*, adaxial lamella of inner gill-plate; *fr*, reflected lamella of inner gill-plate; *g*, line of concrescence of the reflected lamellae of the two inner gill-plates; *h*, rectum; *i*, supra-branchial space of the sub-pallial chamber. (After Lankester.)

In one whole group, the Septibranchia, this branchial partition loses its normal structure in consequence of a predominant development of its contractile elements, by which it is converted into a muscular septum perforated by apertures leading ventro-dorsally (Fig. 211). The water passes through these apertures from the infra-branchial into the supra-branchial or cloacal chamber. Respiration is effected in the latter chamber by the internal surface of the mantle, which is bathed by a strong current of water passed through by the contractions of the muscular septum.

As regards the structure of the gills, it has been known since 1877 (Peck) that in all the Lamellibranchia each constituent filament of the gill is clothed externally by an epithelial layer continuous with the epithelium of the general surface of the body.

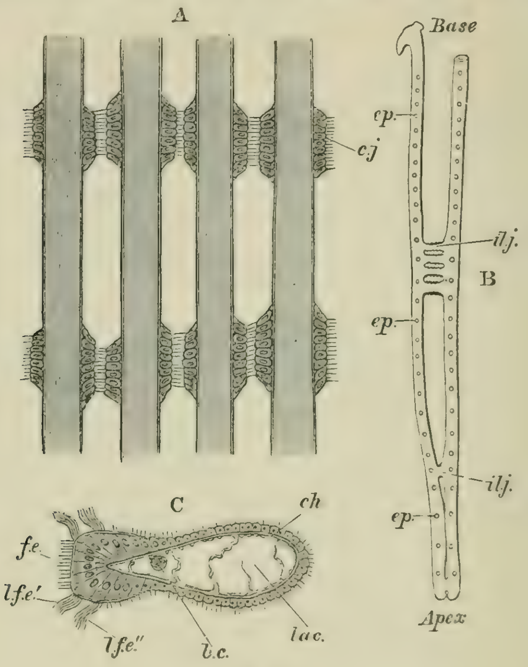

FIG. 210.

Ctenidial filaments of *Mytilus edulis*. *A*, part of four filaments seen from the outer face in order to show the ciliated junctions *c.j*. *B*, diagram of the posterior face of a single complete filament with descending (direct) ramus and ascending (reflected) ramus ending in a hook-like process; *ep*, the ciliated junctions; *i.l.j*, inter-lamellar junction. *C*, transverse section of a filament taken so as to cut neither a ciliated junction nor an inter-lamellar junction; *b.c*, blood corpuscle; *ch*, chitinous tubular lining of the filament; *f.e*, frontal epithelium; *l.f.e'*, ciliated edge-cells; *l.f.e''*, lateral cells with long cilia; *lac*, blood lacuna traversed by a few processes of connective tissue cells. (From Lankester, after Holman Peck.)

At certain points this epithelium is modified and bears powerful cilia, particularly on the two ventral edges of each filament, where the so-called "corner cells" (Fig. 210, *l.f.e'*), by the action of their cilia, keep up a brisk current of water over the surface of the gills. There are also "lateral" ciliated cells on the two faces of each filament, which ensure the ciliary union between successive filaments. Internally each filament presents a supporting structure, formed by paired longitudinal thickenings of the sub-epithelial connective tissue. This thickening is specially well developed on the internal sides of the lamellae in the Anomiidae, Arcidae, and Trigoniidae (Filibranchia, in which the filaments are very loosely held together), while in the rest of the Lamellibranchia the thickening is most developed on the external or ventral side.

The cavity of the branchial filaments is divided lengthwise by a connective tissue septum in the Anomiidae, Arcidae, and in *Pecten*. The afferent branchial vessel runs in the dorsal half of the axis in the Protobranchia, and consequently the blood enters each filament on the dorsal side and passes to the ventral side to enter the efferent branchial vessel leading to the auricle. Thus in each filament there are two currents running in opposite directions, but continuous with one another. The same thing may be seen in the narrow and still independent filaments of the Anomiidae and Arcidae, but when the cavities of successive filaments are put into communication with one another along the free borders of the reflected lamellae, there is but one current in each filament running from the afferent vessel (whose position is variable) to the efferent vessel common to the two gill-plates.

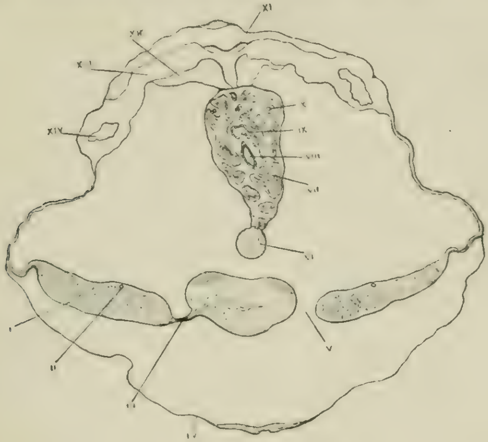

FIG. 211.

Transverse section of *Cuspidaria*, taken through the heart. I, branchial septum; II, branchial nerve; III, sphincter of branchial orifice; IV, mantle; V, septal orifice; VI, posterior retractor of the foot; VII, testis; VIII, intestine; IX, accessory genital gland; X, visceral commissure; XI, ventricle; XII, pericardium; XIII, auricle; XIV, kidney.

In addition to their respiratory function, the gills are accessory to the function of alimentation. The action of their cilia produces a constant current from behind forwards, which carries particles suspended in the water towards the labial palps, and consequently towards the mouth. In some rare cases—for example, in *Mytilus*—an accessory respiratory apparatus is developed in addition to and outside the ctenidial branchiae, in the form of little secondary pallial outgrowths, constituting the folded organs called "frills."

3. *Excretory Organs.*—The principal excretory organs are the kidneys, which are symmetrical organs situated below the pericardium in the postero-dorsal region of the body: they generally extend back to the posterior adductor muscle, but not so far in the Protobranchia (Fig. 231, *k*). They have the form of two sacs, with glandular walls, irrigated by the venous blood passing to the gills and opening on the one hand into the pallial cavity by orifices situated at their anterior ends and external to the visceral commissure, and on the other hand into the pericardium. This latter organ is a median dorsal pouch, situated in the posterior part of the visceral mass and enclosing the heart (Fig. 204, I; 205, *p*). In the Anomidae alone of all the Lamellibranchia the pericardium is greatly reduced, does not contain the heart, and consists of two small ramified spaces. The pericardium communicates with the kidneys by two symmetrical ventral reno-pericardial or internal renal orifices (Fig. 212, *rp*), and in *Anomia* the kidneys communicate with the two small ramified spaces mentioned above. The tubes of the gland of Keber, which ramify in the mantle, also open into the pericardium. The pericardium is always completely shut off from the circulatory system, a fact which can readily be demonstrated in Lamellibranchs with red blood.

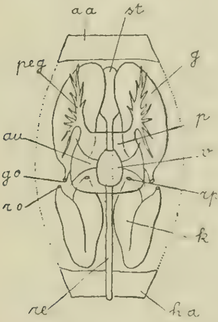

FIG. 212.

Diagram of the pericardial organs in the Lamellibranchia, dorsal aspect. *a.a*, anterior adductor; *au*, auricle; *g*, right genital gland; *g.o*, genital orifice; *h.a*, posterior adductor; *k*, right kidney; *p*, pericardium; *pe.g*, pericardial gland; *re*, rectum; *r.o*, renal opening; *rp*, renopericardial orifice; *st*, stomach; *v*, ventricle.

The structure of the kidneys is simplest in the Protobranchia. In this group each kidney has the form of a more or less cylindrical sac folded on itself in such a manner that the pericardial and external orifices are both anterior. The lumen of the sac is large, its wall is glandular and uniform throughout its extent, and the two kidneys do not communicate with one another (*Solenomya*, Fig. 213). This essential character of a tube folded into a U-shape, so that one branch is antero-posterior and the other postero-anterior, is preserved throughout the Lamellibranchia, but as a result of specialisation the interior surfaces of the renal sacs are more and more increased by the formation of multiple folds, giving a spongy appearance to the organs. Sometimes, also, the terminal part or postero-anterior branch loses its excretory character and is modified to form a simple duct, which more or less surrounds the other branch (Unionidae, Fig. 242 (6), *on*, *or*).

In other cases the differentiation into two branches folded one over the other disappears through the reduction of the antero-posterior branch; the kidney is then a simple sac into which the reno-pericardial duct opens. This may be seen in some Filibranchia.

The two kidneys do not communicate with one another in *Solenomya* and in many Filibranchia, but a communication between their anterior ends is already present in *Yoldia* and *Leda*, and a communication, often of considerable extent, between their posterior ends is found in the majority of the more specialised forms, *e.g.* *Modiolarca*, *Lasaea*, *Donax*, *Tapes*, *Pseudokellya*, and especially in the Myacea, Pholadidae, and Anatinacea. The renal organs are excessively ramified and extend over the whole surface of the visceral mass in *Ostraea*, and both in this genus and in *Pholas* they surround the posterior adductor muscle. The kidneys similarly extend very far forward in *Mytilus* and in the majority of the Anatinacea, penetrating into the mantle itself in *Lyonsiella*. Finally, in the Septibranchia the kidneys are almost wholly immersed in the pallial sinus (Fig. 211, XIV).

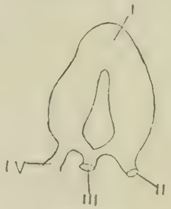

FIG. 213.

Left kidney of *Solenomya mediterranea*, ventral aspect. I, posterior part of the kidney; II, renal external pore; III, reno-pericardial orifice; IV, duct of the gonad.

In the most archaic Lamellibranchia the renal secretion is passed out of the body in a liquid form, but in others in the form of solid concretions, exhibiting concentric layers of growth, and in normal conditions containing only urea.

The excretory function is carried out by the pericardial glands as well as by the kidneys. These glands are differentiations of the epithelial wall of the pericardium, and may be localised on and impart a brownish tint to the auricles, as in many Filibranchia (Arcidae, Mytilidae, Pectinidae) and the Ostraeacea, or they may be near the auricles as in the Aviculidae. In this condition they are less well developed in the more specialised groups, but they reappear in *Pholas* and *Saxicava*. The glands frequently exist in the form of a glandular lining of the anterior part of the pericardium or of the glandular diverticula which pass from the pericardium into the mantle (Fig. 212, *pe.g*). This arrangement may be seen in the Unionidae—the diverticula constituting the "organ of Keber"—in certain Lucinidae, Veneridae (Fig. 202, *pe.g*), Tellinidae, *Solen*, *Pholas*, and *Aspergillum*. In the last-named genus these diverticula used to be called pericardial veins at a time when the pericardium was thought to be a blood sinus. The pericardial glands excrete hippuric acid, which is poured into the pericardium, and from thence passes into the kidneys.

4. *Nervous System and Sense-Organs.*—The different pairs of nerve-centres are always placed at some distance from one another in the

Lamellibranchia. In the Protobranchia alone are there four distinct pairs of ganglia, cerebral, pleural, pedal, and visceral, in the adult (Fig. 214). In this group there is a pleural ganglion attached to the cerebral ganglion on either side, as is the case in the Scaphopoda and the "epiathroid" Gastropoda (Figs. 182; 123, B). There are therefore two pedal connectives on each side (*Solenomya* and *Nucula*), namely, the cerebro-pedal and the pleuro-pedal connectives, which are free in the initial part of their course (Fig. 214, *c.p.c*, *pl.p.c*), but are fused together half-way towards the pedal centres in *Nucula*, and for nearly the whole of their length in *Solenomya*, as is the case in *Dentalium* (Fig. 182) and the Atlantidae. In all other Lamellibranchia the pleural centres are intimately fused with the cerebral, and there is only a single pedal connective on each side (Fig. 215, B). Nevertheless, in all the Lamellibranchs belonging to different groups that have been studied from this point of view, a pleural ganglion distinct from the cerebral has been recognised in the course of development (*Modiolarca*, *Dreissensia*, *Lasaea*, *Teredo*).

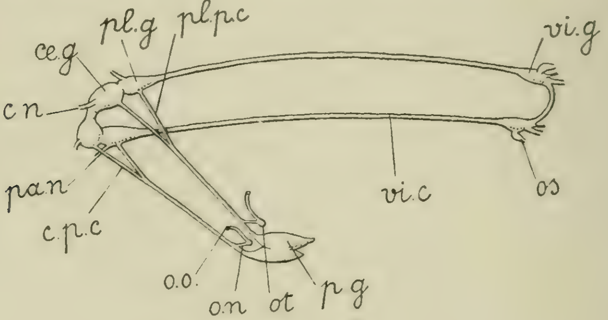

FIG. 214.

Nervous system of *Nucula nucleus*, viewed from the left side, and a little ventrally. *ce.g*, cerebral ganglion; *c.n*, cerebral nerve; *c.p.c*, cerebro-pedal connective; *o.n*, otocystic nerve; *o.o*, otocystic orifice; *os*, osphradium; *ot*, otocyst; *pa.n*, pallial nerve; *p.g*, pedal ganglion; *pl.g*, pleural ganglion; *pl.p.c*, pleuro-pedal connective; *vi.c*, visceral commissure; *vi.g*, visceral ganglion.

In all the Lamellibranchia the cerebral, or rather the cerebro-pleural, centres are connected with the pedal and visceral centres: thus there are two distinct commissures, the pedal and the visceral. In *Mytilus*, however, the visceral commissure is fused for a certain distance with the pedal connectives. The visceral commissure is always long, and issues from the pleural ganglia in *Nucula* and *Solenomya*, from the cerebro-pleural ganglia in other Lamellibranchia. It runs somewhat superficially right round the viscero-pedal mass, inside the renal orifices (Fig. 231, *r.o*), and bears on the posterior part of its course a large pair of ganglia

(Fig. 215, *c*), and in exceptional cases a little ganglion at about the middle of its length on either side, at the point of origin of the branchial, pallial, or visceral nerves. These additional ganglia occur in *Dreissensia* and in some other genera of Eulamellibranchia, viz. the Unionidae, *Cardium*, *Lutraria*, *Mya*, and *Solen*. Each of the three chief pairs of ganglia presents the same general characters in the entire class, and special characters in certain forms.

The cerebro-pleural ganglia are supraoesophageal and are situated above the buccal orifice; generally on the posterior face of the anterior adductor muscle when this exists (Figs. 230, 251, *c.g*). In the Solenomyidae alone do they occupy a more posterior position (Fig. 231, *c.g*). In the Protobranchia, and in *Mactra corallina* and *Venus*, the cerebro-pleural ganglia are attached to one another, but in all other forms they stand apart. They innervate the labial palps, the anterior adductor muscle, and the anterior part of the mantle, and send fibres to the osphradia and otocysts.

The pedal ganglia are situated in the mass of the foot at a greater or less distance from the cerebral centres; they are always attached to one another (Figs. 214, *p.g*; 215, *b*). When the foot is atrophied they become more and more reduced—*e.g.* in *Teredo* (Fig. 195, *p.g*), *Ostraea*, *Pecten* (Fig. 215, C)—and the pedal connectives become very short.

The visceral ganglia are situated some distance behind the posterior adductor muscle in all the Protobranchia (Fig. 231, *v.g*), but in other Lamellibranchia they are to be found on the ventral face of this muscle (Figs. 188, 218, 219, etc., *v.g*), except in *Thracia*, in which they are in front of it, and in some highly specialised forms in which they are again behind it, as, for example, in *Pholas*, and particularly in *Teredo*, in which the posterior adductor is shifted forward (Fig. 195, *v.g*). The visceral ganglia are generally superficial, and barely covered by the tegumentary epithelium (Figs. 188, 236), but in *Lima* they are somewhat deeply embedded in the visceral mass. The two ganglia are primitively distant

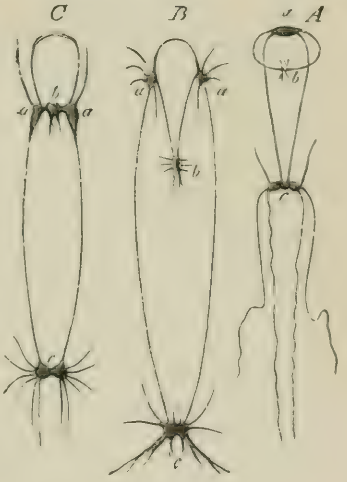

FIG. 215.

Central nervous system. *A*, of *Teredo*; *B*, of *Anodonta*; *C*, of *Pecten*. *a*, cerebral ganglion-pair; *b*, pedal ganglion-pair; *c*, visceral ganglion-pair. (From Lankester, after Gegenbaur.)

from one another, and remain so in most Protobranchia (Fig. 214, *vi.g*), in the Anomiidae, most species of *Arca* (Fig. 188, *v.g*), in *Adacnarca* and *Philobrya*, the majority of the Mytilidae, *Avicula* (Fig. 236), *Ostraea*, and certain Lucinidae (*Montacuta*). On the other hand, they are in juxtaposition in *Yoldia*, *Pectunculus*, *Limopsis*, certain species of *Arca*, the Trigoniidae, *Modiolaria*, the Pectinidae, most Eulamellibranchia, and the Septibranchia. The visceral centres innervate the gills, the heart (by recurrent nerves passing round the posterior adductor muscle), the posterior part of the mantle, and the siphons. The anterior pallial nerves issuing from the cerebro-pleural centres and running along the borders of the mantle anastomose with nerves issuing from the visceral ganglia to form a complete pallial circle on either side. In some Eulamellibranchia (*Dreissensia*, Pholadidae, and Teredinidae) there is a small but distinct ganglion mass in front of the visceral ganglia, and united to the two branches of the visceral commissure. In *Dreissensia* this accessory ganglion gives off several nerves, chiefly to the viscera.

The Lamellibranchia have no differentiated stomato-gastric system; the median faces of the two branches of the visceral commissure give rise to nervous strands which pass to the alimentary canal.

Tactile sensibility is specially localised in the most exposed parts of the body, that is to say, in the borders of the mantle along which run the circumpallial nerves formed by the anastomosis of the anterior pallial nerves from the cerebro-pleural ganglia with nervous trunks issuing from the visceral centre. The mantle borders very often bear sensory papillae, or more or less well developed tentacles throughout their extent, *e.g.* in *Solenomya* (Fig. 231, *pa*), *Lepton*, *Pecten* (Fig. 235, *pa*), and above all *Lima*: in this last genus the tentacles are long, contractile, and disposed in several rows. When the borders of the mantle are fused together at various points, these sensory papillae are localised at the posterior ends, at the place of entrance of the respiratory fluid, or at the margins of the siphons (Figs. 219, 221), or round the two siphons to form a sort of tentacular crown, as may be seen, for example, in *Cardium* (Fig. 243, *a.s*, *br.s*), *Tapes*, *Corbula*, *Poromya* (Fig. 249, *p.t*). In some cases there are highly developed tentacles; thus in *Lepton* and *Galeomma* there is a median azygos tentacle at the anterior end at the point of union of the two mantle lobes, and two symmetrical tentacles in the same situation in *Solen*. There are two symmetrical tentacles at the posterior end in *Solenomya*, and a single lateral tentacle on the right or left side in the Ledidae (*Yoldia*, Fig. 230, *s.t*, *Leda*, and *Malletia*). The labial palps are not highly specialised tactile organs, and serve as accessory alimentary rather than sensory organs.

At the origin of each great branchial nerve, close to the visceral ganglion—and consequently on the posterior adductor muscle in most cases—there is an accessory ganglion (Fig. 214, *os*), above which the tegumentary epithelium is modified to form a sensory organ, and is often pigmented, as for example in *Arca*. This organ corresponds to the *osphradium* of the Gastropoda, and its situation at the point of attachment of the gill renders it probable that it serves to test the respiratory fluid. The osphradial ganglion receives nerve-fibres not from the visceral ganglion, but from the cerebral ganglion by way of the visceral commissure.

Another organ of an analogous nature, lying on the posterior adductor muscle on either side of the anus (and consequently behind the osphradia), is found in many asiphonate forms, for example, in the Arcidae, the Trigoniidae, the Pectinidae, and the Aviculidae. It forms a little papilla or epithelial elevation at the end of a nerve strand given off from the posterior pallial nerve, which in turn is given off from the visceral ganglion. In these Lamellibranchs the two little organs in question often show a tendency to asymmetry, that of the right side being better developed than that of the left. In the siphonate Lamellibranchia, in which the gills are united together posteriorly and conceal the posterior adductor muscle, the sensory organ in question is displaced along the course of the posterior pallial nerve, and lies at the internal end of the inhalent or branchial siphon, often lying over a "siphonal" ganglion developed at this place. In such case the organ may be an epithelial projection in the form of a glandular and sensory plate (*Leda*, *Donax*, and *Pholas*), or a projecting lamina (*Mactra*, *Scrobicularia*, etc.), or even a tuft composed of many papillae (*Tellina*). Lastly, an adoral sense-organ, provided with an accessory ganglion, exists in the neighbourhood of the palps in *Nucula* and *Poromya*.

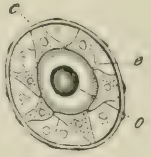

Fig. 216.

Otocyst of *Cyclas*. *c*, capsule; *e*, ciliated cells lining the otocystic capsule; *o*, otolith. (From Lankester, after Leydig.)

The otocysts or statocysts, as is the case in the majority of the Mollusca, are situated in the pedal mass in proximity to the pedal ganglia (Figs. 230, *ot*; 242, *ay*), and they may even be deeply embedded in these centres, for instance, in *Galeomma*, and the Leptonidae (*Lasaea*, *Kellya*). In the majority of the Protobranchia (*Nucula*, *Leda*, *Solenomya*), in *Arca*, and in some Mytilidae (*Mytilus*, *Lithodomus*) these organs are simply deep invaginations (otocrypts) of the superficial epithelium of the foot, and communicate with the exterior by a fine canal which opens on the side of and in the dorsal region of the foot (Fig. 214, *ot*, *o.o*): this canal is closed in the adult *Yoldia*. In the adult *Solenomya* the otocysts have disappeared. In *Leda* they each contain an otolith, but in *Nucula*, *Arca*, and the Mytilidae they contain numerous irregularly-shaped auditory particles. In the rest of the Lamellibranchia the otocysts are completely closed spherical cavities, containing a number of auditory particles (otoconia) in the Filibranchia, but a single large otolith in the Eulamellibranchia and Septibranchia, with the exception of *Saxicava* and the Anatinacea, in which both otoconia and an otolith coexist in each otocyst. In *Ostraea* both otoliths and otoconia appear to be absent.

The cavity of the otocyst is generally lined with ciliated cells (Fig. 216, *c*), but cilia may be absent in forms which have otoliths. The nerves supplying the otocysts do not originate from the pedal ganglia, but are branches of the cerebro-pedal connectives (Fig. 214, *o.n*), and their fibres can be traced back to the cerebral ganglia. As regards the physiology of the otocysts, it has been shown that Lamellibranchs—*e.g.* *Anomia*—are able to appreciate sounds transmitted through the water.

Cephalic eyes in the adult state are found only in certain Filibranchia; viz. in the Mytilidae and *Avicula* (Fig. 236, *e*). They are situated at the bases of the first direct filaments of the inner gill-plates, and each consists of a simple pigmented epithelial fossa which contains a cuticular crystalline lens, but they do not seem to confer any great sensibility on the species that possess them. Some other Lamellibranchia have cephalic eyes during larval life: they are situated outside the velum, like the eyes of the larvae of Polyplacophora. One may suppose that the mantle and the shell, which cover up the whole of the body, render cephalic eyes of little use. Further, by way of organic counterpoise one finds that the absence of cephalic eyes is compensated by the development of analogous organs on the only parts of the body that can be projected from the shell, that is to say, on the edges of the mantle and the siphons. The most simple arrangement consists in the presence of pigmented cells at the extremities of the siphons or around the posterior pallial apertures, the existence of such cells coinciding with an increased photodermatic sensibility whether for both a sudden illumination and a sudden obscuration as in *Pholas*, *Lithodomus*, *Mactra helvacea*, and *Tellina complanata*; or for a sudden obscuration only, as in *Ostraea* and certain species of *Cardium* and *Venus*; or for an increase of illumination, as in *Lima* and *Psammobia vespertina*. As the result of specialisation, pigment spots of this kind are transformed into veritable eyes, situated on the projecting edges of the mantle and siphons.

Pallial eyes arising in this manner are of several different kinds, of which the principal are those occurring in the Arcidae, *Lima*, and the Pectinidae, *Spondylus*, and some species of *Cardium*.

In the greater number of Arcidae, namely, in the genus *Arca*, except *A. diluvii*, and in *Pectunculus*, the pallial eyes are but little differentiated in structure, but are collected in groups; that is to say, they are compound or faceted eyes, each element of which is a pigmented cell or ommatidium with a cuticular cornea. In *Lima excavata* (*L. hians* and *L. loscombii* have no eyes) there are from eighteen to twenty-three eyes on the border of each mantle flap, consisting of very deep pigmented fossae, at the bottom of each of which there is a layer of rods and a refractive body.

In *Pecten* (with the exception of abyssal species) and *Spondylus* the eyes have a more complicated structure: they are isolated and always in larger number on the left or superior than on the right or inferior mantle lobe, and they are of different sizes and irregularly arranged. Each eye is borne on a short tentacle projecting from the internal duplicature of the mantle border (Fig. 235, *e*) and its essential structure is that of a sub-epithelial ocular globe. The more superficial moiety of the ocular wall forms the retina in such fashion that the transparent retinal elements have their free extremities turned towards the interior of the globe (Fig. 217, *re*), and each is capped by a cuticular rod. The deeper moiety of the ocular wall, as well as the part of the tentacle surrounding it, is pigmented. In the interior of the ocular cavity there is a refringent layer—the

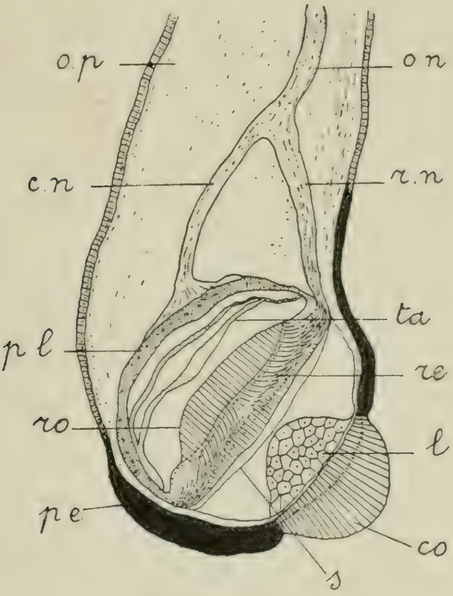

FIG. 217.

Sagittal section of the pallial eye of *Pecten pusio*. *c.n*, complementary optic nerve; *co*, cornea; *l*, crystalline lens; *o.n*, optic nerve; *o.p*, optic peduncle; *p.e*, pigmented epithelium; *p.l*, pigmented layer; *re*, retina; *r.n*, retinal nerve; *ro*, rods; *s*, septum; *ta*, tapetum. (After Rawitz.)

tapetum—of cuticular or secretory origin, which gives the eyes of *Pecten* and *Spondylus* their brilliant lustre. The optic nerve arises from the circumpallial nerve and subdivides: one of its branches passes round the ocular globe to reach the retina. Between the eye and the external corneal epithelium or pellucida there is a cellular lens or conjunctiva, which is extra-ocular and consequently subepithelial. In some cases the corneal epithelium itself is thickened above the eye (Fig. 217, *co*).

In some species of *Cardium*—in *C. rusticum*, for example—the siphons are the only parts of the animal which project from the bottom when the animal is buried, and the tentacles surrounding them are provided with eyes whose structure is analogous to that of the eyes of *Pecten* and *Spondylus*, with this difference, that in the former the pigment is situated in the connective tissue surrounding the ocular globe.

5. *Generative Organs.*—The sexes are separate in the Lamellibranchia in general, but the whole order of Anatinacea is hermaphrodite, and also some small isolated groups, viz. the Cyrenidae, the genera *Poromya*, *Tridacna*, *Kellya*, *Lasaea*, *Entovalva*, and *Scioberetia* (the two last named being parasitic), and certain species of *Pecten*, *Ostraea* and *Cardium*, and *Anodonta imbecilis*. Sexual dimorphism is recognisable only in certain species of *Unio* (*U. batavus* and *U. tumidus*) and in *Lampsilis*, in which the female is rather broader than the male, and in *Astarte*, in which the border of the shell is smooth in the male but crenelated in the female. In the genus *Teredo* there is hyperpolygyny, the males being only in the proportion of 1 : 500 to the females. There is never a copulatory organ, nor yet an accessory gland, unless perhaps in the male *Cuspidaria*. The gonads are paired and symmetrical, superficially placed, and generally occupy the most dorsal and posterior part of the visceral mass, often extending thence into the foot. They are united and communicate with one another in *Donax*, *Lasaea*, *Adacnarca*, *Chlamydoconcha*, *Cuspidaria*, etc. In exceptional cases they extend into the mantle, either into both lobes, as in all the Mytilidae except *Dacrydium* and some species of *Chama*, or into one lobe only as in the Anomiidae. In some genera of Lucinidae, *e.g.* *Montacuta* and *Axinus*, the gonads, together with parts of the liver lobes, project into the pallial cavity in the form of arborescences. Each gonad is an acinous structure and its caeca may be much ramified, for instance, in *Ostraea*.

In the most primitive arrangement there is no proper generative aperture; each gonad discharges its products into the reno-pericardial duct, as may be seen in the Protobranchia (*Solenomya*, etc.); but a secondary union between the reno-pericardial duct and the external extremity of the postero-anterior branch of the kidney allows the generative products to pass direct to the external renal orifice (Fig. 213, IV, II). In many other forms the gonad still opens into the kidney of the same side, not near the pericardial orifice, but nearer to the external aperture, *e.g.* in the Anomiidae and Pectinidae, or close to the external orifice, as in *Arca*. In other cases the gonad and the kidney open together into a common slit or cloaca (*Ostraea*, *Cyclas*, Fig. 218, *g.o*, and certain Lucinidae). Finally, in those cases in which there is a separate generative aperture, it may either be situated on a papilla common to it and to the renal orifice (*Mytilus edulis*), or, as is most frequently the case, it may be in the immediate neighbourhood of the renal orifice, and like it, situated to the outside of the visceral commissure (Fig. 242, (6) *g*).

When normal hermaphroditism occurs in the Lamellibranchia, it may exist in one of the following different forms. In the first each gonad is entirely hermaphrodite throughout its extent; that is to say, uniformly composed of acini capable of producing ova and spermatozoa simultaneously or successively. This condition is found in *Ostraea edulis*, *O. angasi*, *O. plicata*, *O. lurida* (other species of *Ostraea*, viz. *O. virginica*, *O. glomerata*, and *O. angulata* are dioecious), *Kellya*, and *Lasaea*. In the second form there are male and female acini lying side by side throughout the whole extent of the gonad, *e.g.* *Tridacna*, *Cardium oblongum*, and *C. norvegicum*. In the third form the gonads are differentiated into regions of different sex, the anterior region being male and the posterior female (Fig. 235, *t*, *ov*), but these are not separate from one another, and have a common duct and a single orifice: this is the case in *Pecten hermaphroditus*, *P. maximus*, *P. jacobaeus*, *P. opercularis*, *P. glaber*, *P. irradians*, and *P. flexuosus* (*P. inflexus* and *P. varius* are dioecious). The same arrangement is found in the Cyrenidae (*Cyclas*, etc.), in which,

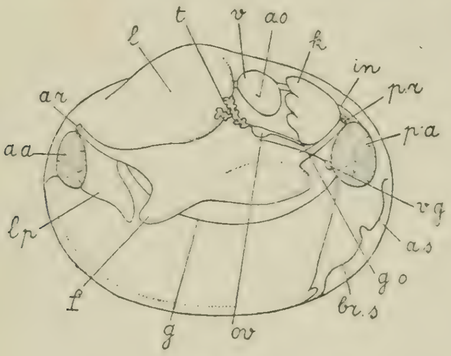

FIG. 218.

Cyclas, left-side view, after removal of the left pallial lobe, gill, and auricle. *a.a*, anterior adductor; *a.o*, auriculo-ventricular orifice; *a.r*, anterior foot retractor; *a.s*, anal siphon; *br.s*, branchial siphon; *f*, foot; *g*, right gill; *g.o*, genital orifice; *in*, intestine; *k*, left kidney; *l*, liver; *ov*, ovary; *p.a*, posterior adductor; *p.r*, posterior foot retractor; *t*, testis; *v*, heart-ventricle; *v.g*, visceral ganglion and commissure (posterior part).

however, the male and female portions of the gonad are not actually contiguous, but are united by a short canal (Fig. 218, *t*, *ov*), so that the spermatozoa have to pass through the ovarian cavity before they are eliminated. Finally, in the fourth mode, an ovary and a testis completely separated from one another exist on either side of the body, each having its own proper duct and external orifice. This is the case in all the genera forming the order Anatinacea and in *Poromya* among the Septibranchia. In these forms the ovary is dorsal and posterior, the testis more anterior and ventral (Fig. 219, *t.o*). The male and female genital orifices of the same side are contiguous; they open on a common papilla in the Anatinacea, but the female aperture is outside the visceral commissure, and therefore in the normal and original position of the Lamellibranch genital orifice, whereas the male aperture is within the visceral commissure. In *Poromya* the male and female ducts of each side open into a common orifice, external to the visceral commissure. In all these hermaphrodites the male products are the first to ripen. Accidental cases of hermaphroditism have been met with in dioecious Lamellibranchs (*Mytilus*, Unionidae), and a unisexual individual of the normally hermaphrodite species *Pecten glaber* has also been described.

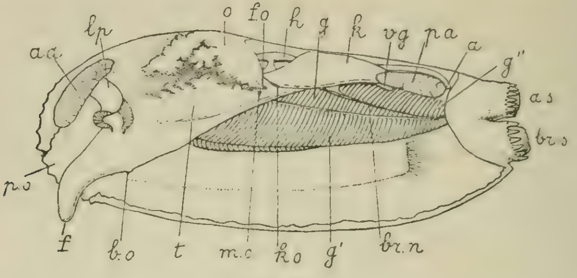

FIG. 219.

Lyonsia norvegica, left-side view after removal of left pallial lobe and left gill. *a*, anus; *a.a*, anterior adductor; *a.s*, anal siphon; *b.o*, byssal orifice; *br.n*, branchial nerve; *br.s*, branchial siphon; *f.o*, female orifice; *g*, gill (direct internal lamina); *g'*, reflected internal lamina of the right gill; *g''*, outer plate of the gill; *l.p*, labial palp.; *m.o*, male orifice; *o*, ovary; *p.a*, posterior adductor; *p.o*, pedal orifice of the mantle; *t*, testis; *v.g*, visceral ganglion.

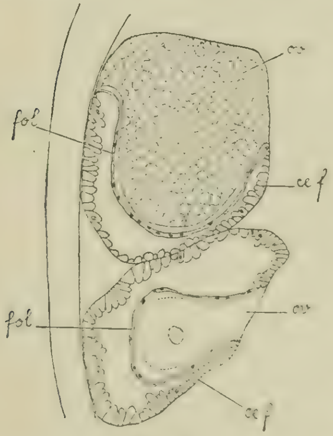

FIG. 220.

Pseudokellya cardiformis, section of a part of the ovary. *ce.f*, follicular cells; *fol*, ovular follicle; *ov*, ovarian egg.

The testis of a male or hermaphrodite is always readily recognisable by its brilliant white colour; on the other hand, the ovary is often red (*Mactra*, *Donax*, etc.). The ovum is derived from a cell of the ovarian epithelium, but in most cases the neighbouring cells contribute to the formation of its vitellus (*Cyclas*, etc.). The ovum is surrounded by a vitelline membrane, which is often fairly thick (Unionidae, Anatinacea, etc.), and is only interrupted at the micropyle, or point of attachment to the ovarian wall. It is at this point that the spermatozoon effects an entrance. The vitelline membrane disappears after the first stages of segmentation, except in incubatory forms. A true ovarian follicle, formed of a continuous and regular envelope of epithelial cells, has been described only in *Pseudokellya* (Fig. 220, *fol*).

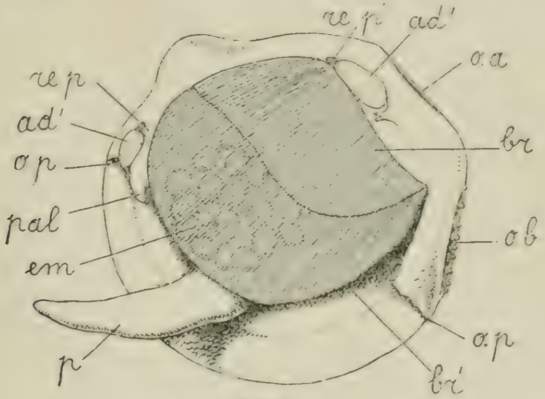

FIG. 221.

Pseudokellya cardiformis, Smith, left-side view (the left pallial lobe removed). *ad'*, *ad''*, anterior and posterior adductor muscles; *br*, *br'*, internal and external gill-plates; *em*, embryos in the internal gill-plate; *o.a*, anal orifice of the mantle; *o.b*, branchial orifice of the mantle; *o.p*, limits of the pedal orifice of the mantle; *p*, foot; *pal*, labial palp; *rep*, *rep'*, anterior and posterior foot-retractor.

III. EMBRYOLOGY.

Viviparous Lamellibranchs are unknown, but some few appear to be viviparous because they are incubatory. This is the case in some Filibranchia (*Arca vivipara* and *Philobrya*) and in many Eulamellibranchia, principally in the Submytilacea (certain species of *Ostraea*, *Condylocardia*, *Lasaea*, *Bornia*, *Scioberetia*, *Entovalva*, *Thecalia*, Unionidae, Cyrenidae, *Pseudokellya*, *Teredo*, etc.). The ova then are hatched after their escape from the genital organs, but in the greater number of incubatory forms they are retained for a certain time, in some cases up to the time of hatching, in the interlamellar branchial spaces. In certain Unionidae (*Castalina*, *Arconaia*, *Pseudodon*, etc.) and in *Lasaea* (Fig. 222) and *Pseudokellya* (Fig. 221, *em*) they are retained in the internal interlamellar space, as also in the Cyrenidae (*Cyclas*, etc.), in which special pouches are developed to contain the ova, the maturer ova being the more anterior. In the Unionidae of the Old World and of North America they are retained in the external interlamellar spaces, and in other Unionidae (*Quadrula, Schistodesma, Gibbosula, Cuneopsis*) and in *Modiolaria* in both the external and internal interlamellar spaces. In some other Lamellibranchia, *e.g. Ostraea edulis* and other hermaphrodite species of *Ostraea* such as *O. angasi* and *O. lurida*, and in *Entovalva*, the earlier stages of development are passed through in the pallial cavity, outside the gills. In all other Lamellibranchia the eggs are laid one by one, generally in the spring or summer in temperate climates. In *Nucula delphinodonta* they are collected together in a mucous sac fixed to the posterior part of the shell, and are there incubated.

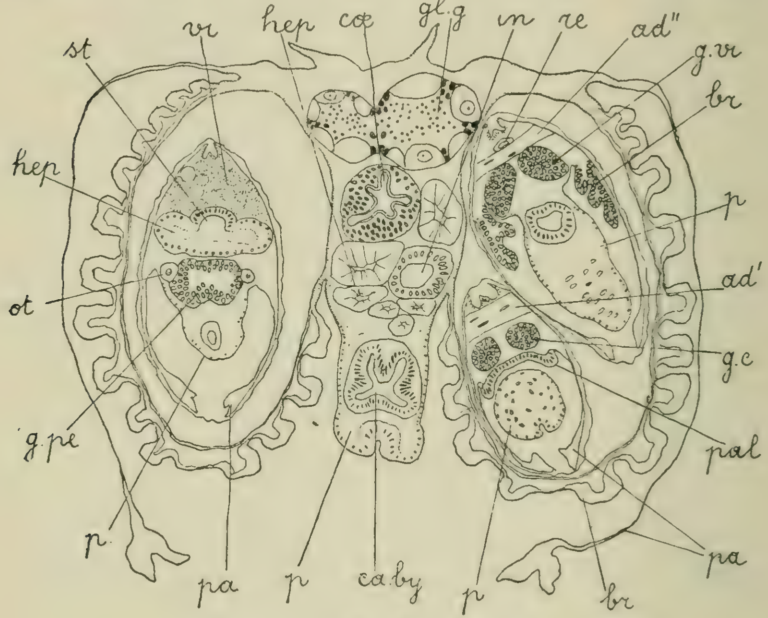

FIG. 222.

Lasaea rubra, a transverse section through the posterior part of the body, showing embryos in the gills. *ad'*, *ad''*, anterior and posterior adductor muscles; *br*, gill; *cae*, caecum; *g.c*, cerebral ganglion; *g.vi*, visceral ganglion; *hep*, liver; *in*, intestine; *ot*, otocyst; *p*, foot; *pa*, mantle; *pal*, labial palp; *st*, stomach; *vi*, vitellus.

Fertilisation may be effected externally to the maternal parent, as, for instance, in *Pecten*, the dioecious species of *Ostraea*, *Modiolaria*, *Dreissensia*, *Mactra*, *Pholas*, etc., and in all these forms artificial fertilisation is possible; or it may be effected in the pallial cavity, in the cloacal or suprabranchial chamber, as in *Cardium* and several other incubatory forms, or in the oviduct itself in *Ostraea edulis*.

The formative pole of the ovum is opposite to the micropylar end. The segmentation is unequal from the first cleavage onwards. The macromere formed at the first cleavage is loaded with yolk granules and remains single for a long time, but gives rise to the three first groups of micromeres, which partly cover it as with a cap (Fig. 9, C). Finally, the macromere divides to form the endoderm cells. The gastrula is rarely formed by invagination (*Pisidium*, Ray Lankester), but in nearly all cases by epiboly, or sometimes by a process midway between the two, in which there is at first an epiboly resulting from the multiplication of the small ectodermic cells surrounding the single macromere, and finally an invagination after division of the macromere. This process is found in *Ostraea*, *Cyclas*, and the Unionidae, and in the two last-named the segmentation cavity is very large and the enteron small (Fig. 227). The blastopore remains open in some cases, *e.g.* in *Ostraea*, but closes in *Cyclas*, *Pisidium*, the Unionidae, *Dreissensia*, *Teredo*, etc. But the mouth and oesophagus are soon formed by a secondary ectodermic invagination at the point of closure of the blastopore. The yolk remains in connection with the dorsal surface of the enteron and is slowly absorbed. The endoderm gives rise to the stomach and the two liver lobes and to the intestine; the liver lobes often display a marked asymmetry, the left lobe being larger than the right in *Mytilus*, *Dreissensia*, and *Yoldia*. The anal ectodermic invagination placing the intestine in communication with the exterior is generally at the extreme posterior end of the embryo, is very short, and very late in appearance. The mesoderm originates, at an early period, from the most posterior of the four primary endoderm cells; the resulting mesomeres take up a position between the ectoderm and endoderm in the form of two symmetrical mesoderm bands.

In its general characters the development of the Lamellibranchia conforms to the type observed in the other classes of the Mollusca, but a certain number of special features must be noted. (1) The *shell-gland* makes its appearance at an early period in the normal position; that is to say, at the formative pole, nearly opposite to the blastopore (Fig. 223, *sk*). It is single, like the shell-gland of all other Molluscs. During its extension it gives rise to a saddle-shaped cuticular pellicle, which becomes calcified at two symmetrical points, right and left of the middle line. These two centres of calcification eventually form the two valves of the shell, but, except in the Unionidae, they do not develop as fast as the subjacent lobes of the mantle. The two valves remain united by the median and dorsal part of the primitively single shell, and the ligament is formed at this line of union.

This condition is reached during the veliger stage; the shell. which is at first too small to contain the whole animal, is called the *prodissoconch*, and is characterised by its two symmetrical valves with a simple linear hinge. After this stage a sudden change is effected in the secretory activity of the mantle, and the embryonic shell or prodissoconch is often separated from the rest of the shell by a more or less projecting ridge, indicating this modification during growth (Fig. 196, *p*). (2) The *velum*, which serves as the larval swimming organ, is a circular outgrowth with

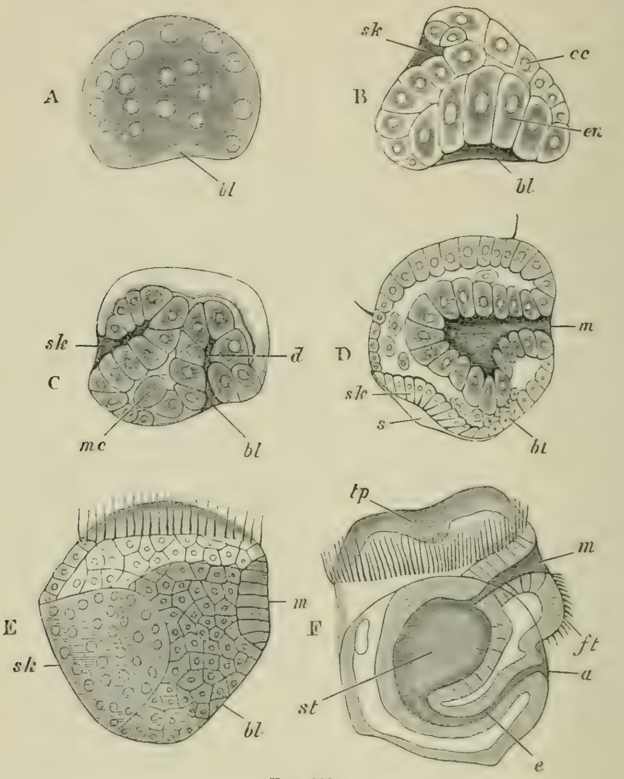

Fig. 223.

Development of *Ostraea edulis*. *A*, blastula stage, with commencing invagination at *bl*, the blastopore. *B*, optical section of a somewhat later stage, in which the invagination of the shell-gland, *sk*, has commenced; *bl*, blastopore; *ec*, ectoderm; *en*, endoderm. *C*, similar optical section of a little later stage. The invagination connected with the blastopore is now more contracted, *d*; and cells, *me*, forming the mesoderm, are separated. *D*, similar section of a latter stage (trochosphere) with closed blastopore *bl*; *m*, the mouth; *s*, shell, on the surface of the shell-gland *sk*. *E*, surface view of an embryo at a period a little more advanced than *D*. *F*, the same embryo seen as a transparent object. *a*, anus; *e*, intestine; *ft*, foot; *m*, mouth; *sk*, shell-gland; *st*, stomach; *tp*, velar area of the prostomium. The extent of the shell and commencing upgrowth of the mantle-skirt is indicated by a line forming a curve from *a* to *F*. On the dorsal side of the stomach is the anterior adductor muscle. (From Lankester, after Horst.)

a ciliated border, lying in front of the blastopore. It is never lobed, and is often provided with a single central flagellum, *e.g.* in *Yoldia* (Fig. 225, *a.c*), the Mytilidae, *Dreissensia* (Fig. 224, *fl*), *Cardium*, *Montacuta*, *Entovalva*, *Mactra*, and *Teredo*, but there is no flagellum in *Pecten*, *Ostraea*, *Avicula*, *Pholas*, *Nucula*, and the Unionidae; it is very much reduced in the incubatory species and quite nul in *Pisidium*. As will be explained further on, the velum may be turned back in such a manner as to cover and adhere to the whole body of the larva, thus giving rise to the "testaceous" larvae peculiar to the Nuculidae. (3) In almost all Lamellibranchs an important invagination is formed near the posterior extremity of the foot: this is the byssogenous cavity (Fig. 224, *by*), which is formed even in species devoid of a byssus in the adult state. In *Cyclas*, for instance, there is a larval byssus by which the embryo attaches itself to the incubatory branchial cavity. (4) In the middle of the velar area there is an apical plate formed by an ectodermic thickening, from which the paired cerebral ganglia originate. In *Yoldia* each cerebral ganglion is formed from a deep tubular invagination, and similarly in *Dreissensia* an apical fossa grows in from the apical plate, and the cerebral centres are formed from its deeper part. The pedal centres arise from ectodermic thickenings between the larval mouth and anus (Fig. 224, *ot*). The pleural ganglia are distinct from the cerebral during larval life, in *Dreissensia*, *Modiolaria*, *Lasaea*, and *Teredo*, at any rate. Two larval eyes with cuticular lenses occur in many forms, on either side the

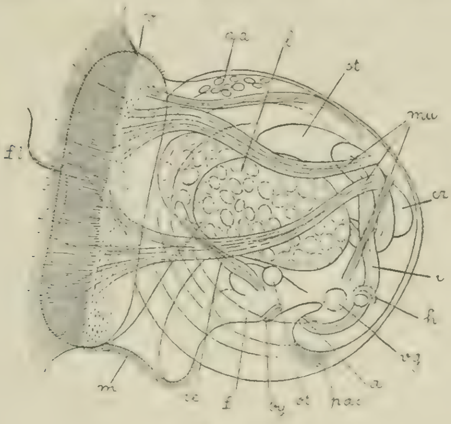

FIG. 224.

Veliger of *Dreissensia polymorpha*, left-side view. *a*, anus; *a.a*, anterior adductor; *by*, byssus gland; *cr*, caecum of the crystalline style; *f*, foot; *fl*, flagellum; *h*, heart; *i*, intestine; *l*, liver; *m*, mouth; *mu*, retractor muscles; *ot*, otocyst and pedal ganglion; *p.a.c*, post-anal cilia; *re*, embryonic kidney; *st*, stomach; *v*, velum; *v.g*, visceral ganglion. (After Meisenheimer.)

velum, at the base of the first internal branchial filament, but their persistence has not been demonstrated except in the Mytilidae and *Avicula* (Fig. 236, *e*). On either side of the pedal centres an ectodermic invagination gives rise to an otocyst; the invaginations close up in most cases, but remain open in *Nucula* and *Mytilus*. The apical portion of the velar area gives rise to the labial palps. (5) In all groups of the Lamellibranchia (Nuculidae, Mytilidae, *Avicula*, *Ostraea*, Fig. 192, *g*, *Dreissensia*, *Entovalva*, *Pisidium*, *Anadonta*, Fig. 228, *br*, etc.), the branchiae originate in the form of filaments, which develop one by one from behind forwards, at the posterior part of the body, on the right and left sides, between the mantle and the visceral mass. The filaments of the internal gill-plate are the first to be formed, afterwards those of the external gill-plate: it is only at a late period that the filaments are reflected and unite with one another. (6) Two *larval kidneys* have been found in several groups (*Dreissensia*, *Cyclas*, *Teredo*), in the form of small organs of ectodermic origin, situated on either side of the anterior end of the larva, behind the velum, and opening to the exterior by their hinder ends (Fig. 224, *re*). Each organ consists of two cells (*Dreissensia*), of which one is deep and ciliated, the other is tubular, with an intra-cellular canal leading from the flagellum of the deeper cell to the external orifice. (7) In the trochosphere or veliger larva provided with a bivalve shell, the anterior adductor muscle is the first to be developed, as may be seen in *Nucula*, the Mytilidae, *Ostraea*, *Pecten*, *Lasaea*, *Entovalva*, *Dreissensia*, *Pisidium*, the Unionidae, *Cardium*, etc. In considering the evolution of the larva one must distinguish between two quite different modes of development, one of which may be called the normal mode, while the other is characterised by the parasitism of the larva and subsequent metamorphoses (Unionidae). In the first mode one may further distinguish a development through a veliger larva, which occurs in most Lamellibranchs, and a development through testaceous larvae, characteristic of the Nuculidae. In the development with a veliger stage, the larva may be free, as is the case in many marine forms and in the freshwater *Dreissensia*, or it may be retained and incubated in the gills, as in *Cyclas*, *Kellya*, *Teredo*, etc. When the larva leads a free existence its velum is always rather prominent (Fig. 224, *v*), but when it is retained and incubated by the parent the velum is reduced or sometimes disappears altogether (*Cyclas*, Unionidae, *Entovalva*). When the velum is absorbed the foot becomes highly developed, even in such forms as become sedentary and fixed in after life, such as *Pecten*, *Avicula*, etc., unless indeed they attach themselves at a very early period.

In the Nuculidae, which have test-larvae, we find that in *Yoldia* and *Nucula proxima* the ova are set free in the water and the larva is free-swimming. But in *Nucula delphinodonta* the female constructs a thin-walled mucoid egg-case, attached to the posterior portion of the shell and in communication with the pallial chamber: into this case the ova are passed as soon as they are laid, and undergo their development. In *Yoldia* and *Nucula proxima* a gastrula is formed by epiboly and then the greater part of the ectoderm gives rise to a "test," which is really a ciliated velum formed in a normal position at the apical pole, but reflected in such a manner as to completely cover the former ectodermic surface of the body—viz. the shell-gland, etc.—leaving only a small opening opposite to the apical plate, in which the stomodaeum and eventually the proctodaeum are formed (Fig. 16). The test consists of five rows of flattened cells, the three median rows bearing circlets of long cilia (Fig. 225). A long ciliated flagellum, like that of many Lamellibranch larvae, is borne in the centre of the apical plate. When the larval development is completed, the test, with its stalk and apical plate, is stripped off and cast away within the space of a few minutes (Fig. 226); the apical cilia shrivelling up and the test cells breaking apart and frequently falling to pieces at once. In the larva of *Nucula delphinodonta* the test is covered with short diffuse cilia, there is no flagellum, and the disruption and casting off of the test occupies several hours, the parts near the apical plate being the last to disappear. The testaceous larvae of the Nuculidae should be compared with the larvae of *Dentalium* (Fig. 15) and of *Myzomenia* (Fig. 17).

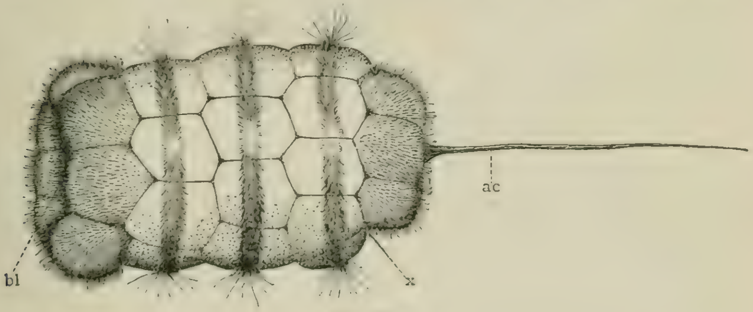

Fig. 225.

Surface view of a forty-five hour embryo of *Yoldia limatula*. *a.c*, apical cilia; *bl*, blastopore; *x*, depression where the cells that form the cerebral ganglia come to the surface. (After Drew.

A development with secondary metamorphosis, acquired in the course of ontogeny, is peculiar to the Unionidae. In this family the eggs are laid in spring or summer, and on leaving the genital orifice pass into the interlamellar space of the internal gill-plate; thence into the interlamellar space of the outer gill-plate by way of the posterior extremity of the gill, where the two spaces communicate with one another behind the branchial axis. In the European Unionidae the eggs are incubated and pass through the earlier stages of their development in the outer gill-plate (see above, p. 226, for an account of the segmentation and endodermic invagination, Fig. 227, II). In *Castalia*, *Arconaia*, *Pseudodon*, etc., the eggs are incubated in the internal gill-plate, and in *Quadrula*, *Schistodesma*, *Gibbosula*, and *Cuneopsis* both gill-plates are used for incubation. The shell-gland, as soon as it is formed, produces a shell which grows as fast as the mantle, and is provided with a large anterior adductor muscle (Fig. 227, I). A ciliated disc, corresponding to the ciliated post-anal surface of *Dreissensia* (Fig. 224, *p.a.c*), is formed behind the blastopore and causes the embryo to rotate in the egg-shell (Fig. 227). These first phases of development take about two months for their accomplishment, and in European Unionidae the embryos hibernate in the interlamellar space without undergoing any appreciable structural modification. In the following spring they are hatched out, and escape through the dorsal or anal pallial aperture in the form of a peculiar larva

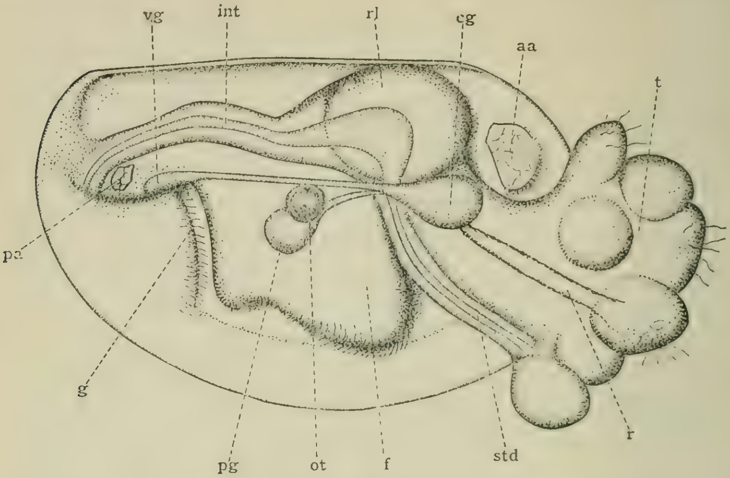

FIG. 226.

Reconstruction of an embryo of *Yoldia limatula* at a stage during "casting," represented as seen from the right side, with the right shell-valve and mantle lobe removed. *a.a*, anterior adductor muscle; *c.g*, cerebral ganglion; *f*, foot; *g*, rudiment of gill; *int*, intestine; *ot*, otocyst; *p.a*, posterior adductor muscle; *p.g*, pedal ganglion; *r*, pouch that leads to the cerebral ganglia; *r.l*, right lobe of the digestive gland; *std*, stomodaeum; *t*, adhering test cells of velum; *v.g*, visceral ganglion. (After Drew.)

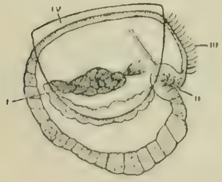

FIG. 227.

Embyro of *Anodonta*, left-side view. I, anterior adductor muscle; II, blastopore; III, posterior ciliated shield; IV, shell. (After Götte.)

called a "glochidium" (Fig. 228). This larva is characterised by the possession of hooks in the middle of the lateral borders of its valves and by its larval byssus—which is not homologous with that of other Lamellibranchs. This byssus appears to issue from, but in reality winds round, the adductor muscle, and originates from a single glandular epithelial cell, deeply embedded in the tissues on the dorsal and anterior side of the muscle. The glochidia swim actively by clapping together the valves of the shell, and eventually attach themselves to the gills or fins of a fish, and become encysted in consequence of a pathological development of the epithelium of their host. This parasitic existence lasts for a period varying from two to six weeks, during which the glochidia are nourished by the epidermic elements of their host, absorbing them by means of the ectodermic cells of the embryonic mantle. During this time most of the definite organs of the adult, the foot, otocysts, gills, etc., which were not required in larval life, are developed, largely as the result of the proliferation of the cells of two symmetrical cavities situated behind the adductor muscle. In a general way the development of the organs follows the normal course, but some—the borders of the mantle, for instance—are formed anew. The glochidium shell is not cast off but persists, though it undergoes a considerable change of shape. The posterior ciliated shield and the byssus disappear. During the early part of the parasitic life the mouth acquires an opening into the previously closed endodermic cavity or archenteron, but the anus is not formed till

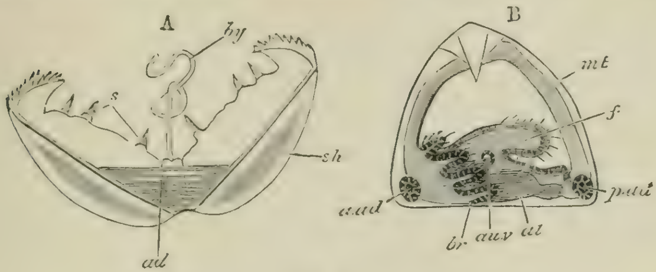

FIG. 228.

Two stages in the development of *Anodonta*; both figures represent the "glochidium" stage. *A*, when free swimming, shows the two dentigerous valves widely open. *B*, a later stage, after fixation to the fin of a fish. *a.ad* and *ad*, anterior adductor muscle; *al*, alimentary canal; *au.v*, otocyst; *br*, branchial filaments; *by*, byssus; *f*, foot; *mt*, mantle-flap; *p.ad*, posterior adductor; *s*, teeth of the shell; *sh*, shell. (From Lankester, after Balfour.)

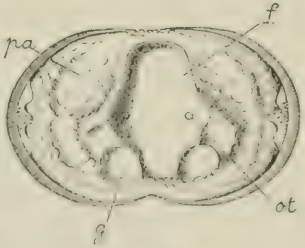

FIG. 229.

Parasitic larva of *Anodonta* on the eighth day of parasitic life; ventral view. *f*, foot; *g*, gill-filaments; *pa*, new mantle; *ot*, otocyst. (After Schierholz.)

the close of parasitic life, and its formation is not accompanied by a sensible ectodermic invagination. When the young *Unio* quits its host its evolution is not complete. The gills continue to grow slowly, their external plates not being developed until the third year, and sexual maturity is not attained until the fifth year, but growth continues for some time after.

IV. Bionomics and Distribution.

All the Lamellibranchia are aquatic. The great majority are marine, but some few families have penetrated into fresh waters. All the members of the class feed upon microscopic organisms, chiefly Diatomaceae and other low forms of plant life. Only the Septibranchia and some other abyssal forms are truly carnivorous.

In general, the Lamellibranchs are burrowing forms, living half-buried in muddy or sandy bottoms, and in this case their plane of symmetry is vertical. But many forms are completely sedentary and are fixed by the byssus, or in a more definitive manner, by the shell itself, as is the case in *Spondylus*, *Ostraea*, *Aetheria*, *Myochama*, etc. In these genera the plane of symmetry becomes horizontal, and the animal usually lies on the right side, *e.g. Pinna*, *Hinnites*, *Spondylus*, *Plicatula*, *Anomia*, and the Rudistae; more rarely on the left side as in *Ostraea*, *Requienia*, and *Chama* generally. Some Lamellibranchs live in holes which they excavate either in wood, as in the case of *Teredo*, or in stone, as *Lithodomus*, *Saxicava*, *Pholas*, *Clavagella*, etc., or even in the shells of other Molluscs. *Lithodomus* is only found in calcareous rocks, and bores its hole by the aid of the acid secretion of glands situated in the antero-dorsal and postero-dorsal regions of the mantle.

Some Lamellibranchs, such as *Lima*, are nidamentous, and construct a nest by means of the byssus. *Lima hians* builds its nest in the space of three weeks, and may afterwards return and reconstruct another from it. *Modiolaria marmorata* and *Entodesma cuneatum* pass their existence deeply buried in the tests of Ascidians, and *Vulsella* lives in a similar manner in sponges; but the few commensalistic or parasitic forms generally live on or in Echinoderms: thus *Montacuta* lives on Spatangids, *Scioberetia* in the incubatory pouch of an Asterid, *Entovalva* in the oesophagus of a *Synapta*. On the other hand, *Ephippodonta* is commensal with a prawn, and certain species of *Lepton* with *Gebia*.

Only a few species are very active: *Tellina*, *Yoldia*, etc., execute leaping movements by forcibly contracting the foot; *Lasaea*, *Cyclas*, etc., crawl on immersed bodies or on the surface of the water; other forms, notably the Pectinidae and Limidae, swim by rapidly opening and closing the valves of the shell; and some elongated forms in which the mantle edges are fused for a considerable extent swim by forcibly expelling water from the posterior aperture of the mantle (*Solen*, *Solenomya*).

In point of size the Lamellibranchs vary from a length of a few millimetres to more than seventy centimetres (*Pinna* and *Tridacna*, some specimens of the latter genus weighing as much as 310 lbs.). The fossil *Hippurites* attained to the length of a metre.

There are more than 5000 living species of Lamellibranchia, of which 1000 are Unionidae. They are distributed all over the world, and some marine forms extend to a depth of 2700 fathoms. Fossil forms appear in the Cambrian, and become very numerous in species from the Silurian onwards. Some large groups, such as the Palaeoconcha of the primary and the Rudistae of the secondary deposits, are quite extinct.

V. Review of the Orders and Families of Lamellibranchia.

The classification of this homogeneous group has long presented great difficulties, for the different organs or apparatus, such as shell, muscles, siphons, etc., that have successively been employed as bases of classification, have not given satisfactory results.

Ray Lankester was the first to suggest (in 1884) that the structure of the gills might furnish characters of classificatory value, and the present writer has constructed on this basis a phylogenetic classification in which the class is divided into five groups. This classification has put various families, such as the Anomiidae, Trigoniidae, Dreissensiidae, etc., into their proper places, and has been largely adopted. Objections to it have, however, been raised, notably by Dall, who has urged that the genera *Euciroa* (Anatinacea) and *Callocardia* (or *Vesicomya*, Cyprinidae) have protobranchiate gills, and that the system of classification according to branchial characters is consequently without foundation. But the recent investigations of Ridewood, undertaken at the instance of Ray Lankester, have shown that it was the objections of Dall that had no foundation: *Euciroa* and *Callocardia* have typical eulamellibranchiate gills.

As the result of the advancement of our knowledge, the classification of the Lamellibranchia founded on the structure of the gills has been ameliorated by the suppression of the order "Pseudolamellibranchia," and the two diphyletic sub-orders which it included, the Pectinacea and the Ostraeacea, may be respectively located in the Filibranchia and the Eulamellibranchia, thus making these two old-established orders correspond to the new orders proposed by Ridewood under the names Eleutherorhabda and Synaptorhabda.

On the other hand, the shell (and particularly its hinge) is the only other organ that has been retained as a basis of the general classification of the Lamellibranchia, especially by palaeontologists, and the subdivisions adopted in this system correspond more or less with those based on the structure of the respiratory organs. Thus the following are very nearly synonymous terms:—

Prionodesmacea = Protobranchia + Filibranchia.
Teleodesmacea = Eulamellibranchia – Anatinacea.
Anomalodesmacea = Septibranchia + Anatinacea.

As regards the value of the last order, Septibranchia, in it the characteristic organs that have given the name to the whole class Lamellibranchia are so profoundly modified, that they differ much more from all the other different kinds of gills than the latter differ from one another, and therefore, even if the Septibranchia should not be placed in contrast to all other Lamellibranchia, they at least constitute a group equivalent to the three other groups, Protobranchia, Filibranchia, and Eulamellibranchia.

Thus the Lamellibranchs are divisible into these four orders. It will be remarked that the numerous studies on the organisation of Lamellibranchia made since 1891, have shown that there has been a progressive evolution in each of these four orders, and that consequently such important organs as the heart, kidneys, and otocysts may exhibit marked differences in relatively nearly related types, and that no strictly pure primitive types have been retained.

From the point of view of phylogeny the most archaic Lamellibranchia are those in which the foot has a "plantar" ventral surface like that of Gastropoda and *Pulsellum* among the Scaphopoda. These archaic forms constitute the Protobranchia (*Solenomya*, Fig. 230, *Yoldia*, Fig. 231, etc.), in which the gonads still retain openings into the initial or pericardial portion of the kidneys, and the branchial filaments are free and not reflected. From these Protobranchia are derived the Filibranchia, whose branchial filaments are reflected, but are still devoid of vascular junctions: these in turn have given rise to the Eulamellibranchia, which are more specialised in respect of the complication of the ctenidia. Finally, eulamellibranchiate forms analogous to the Anatinacea represent the source from which the Septibranchia have been derived.

Order 1. **Protobranchia.**

These are Lamellibranchia whose distinctive character is the possession of gills with flat and non-reflected filaments disposed in two rows on opposite sides of the branchial axis (Fig. 206, A, B). The mantle is provided with a hypobranchial gland lying on the outer side of each gill. The foot has a plantar ventral surface (Fig. 230, *f*) and the byssogenous apparatus is but slightly developed. The nervous system generally presents a distinct pair of pleural ganglia, and the otocysts are generally open. The gut may be provided with a relic of the pharyngeal cavity, which in some cases is furnished with two lateral glandular sacs. The auricles of the heart are muscular; the kidneys are rather simple in structure and glandular throughout their extent. The sexes are separate: the gonads have retained their primitive communications with the initial or internal extremities of the kidneys, but as the two branches of each kidney have acquired a secondary communication at their anterior ends, the genital products pass direct to the external orifice of the kidney by this passage (Fig. 213).

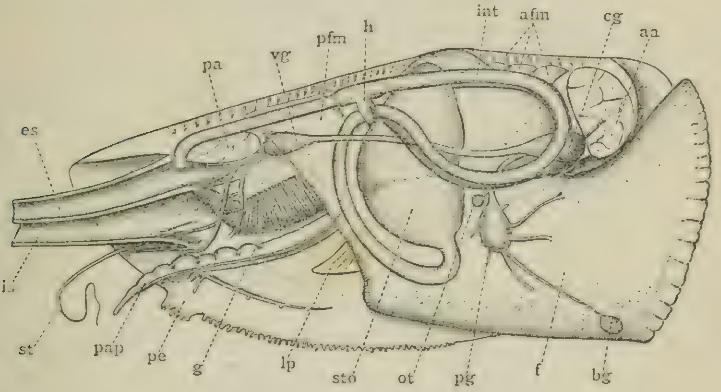

Fig. 230.

Adult specimen of *Yoldia limatula*, represented as seen from the right side, and showing the internal organs. *a.a*, anterior adductor muscle; *a.f.m*, anterior foot muscle; *b.g*, byssal gland; *c.g*, cerebral ganglion; *e.s*, exhalant siphon; *f*, foot; *g*, gill; *h*, heart; *int*, intestine; *i.s*, inhalant siphon; *l.p*, labial palp; *ot*, otocyst; *p.a*, posterior adductor muscle; *pap*, palp appendage; *p.e*, posterior expansion of the margin of the mantle; *p.f.m*, posterior foot muscle; *p.g*, pedal ganglion; *s.t*, siphonal tentacle; *sto*, stomach; *v.g*, visceral ganglion. (After Drew.)

Family 1. Solenomyidae, Gray. In the gills one row of branchial filaments is directed dorsally and the other ventrally (Fig. 231, *g*). The mantle has a long postero-ventral suture, and a single posterior orifice. The labial palps of each side are fused together. The shell is elongate; the hinge has no teeth; the periostracum is thick. Genus—*Solenomya*, Lamarck. Family 2. Nuculidae, Gray. The labial palps free, very broad and provided with a posterior appendage; all the branchial filaments are oriented transversely; the shell has an angular dorsal border and the hinge is pliodont; the mantle is open throughout its extent. Genera—*Nucula*, Lamarck; the heart situated on the dorsal side of the rectum. *Acila*, Adams (Cretaceous, Tertiary, and Recent). *Pronucula*, Hedley. Family 3. Ledidae, Adams. The same characters as the Nuculidae, but the mantle has two posterior sutures and two united siphons; the heart traversed by the rectum. Genera—*Leda*, Schumacher; the mantle borders produced posteriorly into two lobes which simulate a third siphon. *Yoldia*, Moller; siphons elongate;

ligament internal (Figs. 200, 230). *Malletia*, Des Moulins; the ligament external. *Nuculina*, d'Orbigny. FAMILY 4. CTENODONTIDAE, Wöhrmann. An extinct family from the Silurian; the shell is nuculiform and the hinge presents an uninterrupted arcuate row of teeth. Genera—*Ctenodonta*, Salter. *Cuculella*, Fischer. *Cardiolaria*, Meunier-Chalmas.

The fossil group Palaeoconcha, Neumayr, is connected with the Protobranchia through the Solenomyidae. It contains the following families, all of which are extinct:—FAMILY 1. PRAECARDIIDAE, Neumayr Shell equivalve, with the hinge dentition of *Arca*. Genus—*Praecardium*, Barrande; from the Silurian and Devonian. FAMILY 2. ANTIPLEURIDAE, Neumayr. Shell inequivalve; the hinge with an obscure resemblance to that of *Arca*. Genus—*Antipleura*, Barrande; from the Silurian. FAMILY 3. CARDIOLIDAE, Neumayr. Shell equivalve and ventricose; the hinge without teeth. Genus—*Cardiola*, Broderip; from the Silurian and Devonian. FAMILY 4. GRAMMYSIIDAE, Fischer. Shell thin, equivalve, oval, or elongate, the cardinal border thickened but without teeth. Genera—*Grammysia*, Verneuil; from the Silurian and Devonian. *Protomya*, Hall, from the Devonian. *Cardiomorpha*, de Koninck; from the Silurian to the Carboniferous. FAMILY 5. VLASTIDAE, Neumayr. Shell thin, very inequivalve, the hinge without teeth. Genus—*Vlasta*, Barrande; from the Silurian. FAMILY 6. SOLENOPSIDAE, Neumayr. Shell equivalve, thin, greatly elongated, the umbones very far forward. Genus—*Solenopsis*, MacCoy, from the Devonian to the Trias.

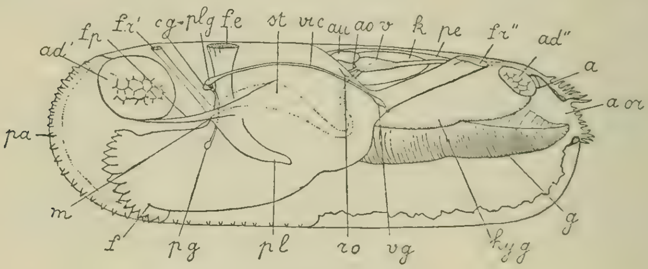

FIG. 231.

Solenomya togata, Poli, left-side view (the left pallial lobe and gill cut away). *a*, anus; *ad'*, *ad''*, anterior and posterior adductor; *ao*, aorta; *a.or*, anal orifice of the mantle; *au*, heart-auricle; *c.g*, cerebral ganglion; *f*, foot; *f.e*, foot elevator; *f.p*, foot protractor; *fr'*, *fr''*, anterior and posterior foot retractor; *g*, right gill; *hy.g*, hypobranchial gland; *k*, kidney; *m*, mouth; *pa*, mantle; *pe*, pericardium; *p.g*, pedal ganglion; *p.l*, palp appendage; *pl.g*, pleural ganglion; *r.o*, renal opening; *st*, stomach; *v*, heart-ventricle; *vi.c*, visceral commissure; *vi.g*, visceral ganglion.

ORDER 2. Filibranchia.

These are Lamellibranchs whose main character is the possession of gills formed of parallel, ventrally directed, and reflected filaments. The successive filaments are joined together by cilia disposed in "ciliated discs" (Figs. 210, A; 232, *i.f.j*). The foot is generally provided with a highly developed byssogenous apparatus. The order comprises five sub-orders—the Anomiacea, Arcacea, Mytilacea, Pectinacea, Dimyacea.

SUB-ORDER 1. ANOMIACEA.

Very asymmetrical animals with a single large posterior adductor muscle. The heart is not contained in the pericardium, lies dorsad of the rectum, projects into the pallial cavity, and gives off a single and anterior aorta. The reflected borders of the inner gill-plates of either side are fused together in the middle line. The gonads open into the kidneys, and the right gonad extends into the mantle. The shell is thin and the animal fixed.

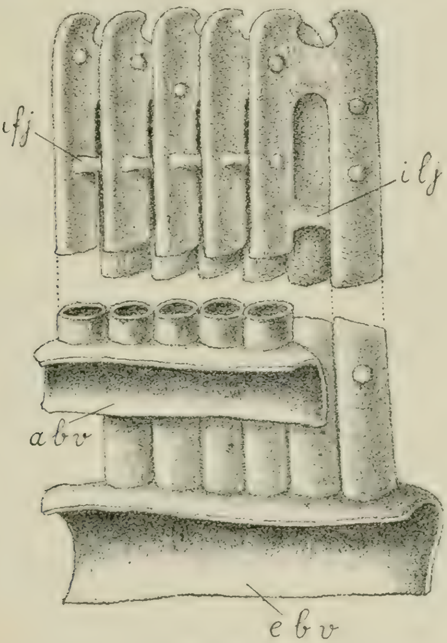

FIG. 232.

A portion of the gill of *Mytilus*, showing the filaments; the median part is cut out. *a.b.v*, afferent branchial vessel; *e.b.v*, efferent branchial vessel; *i.f.j*, interfilamentar ciliated junction; *i.l.j*, interlamellar connective tissue junction. (After Bonnet.)

Family ANOMIIDAE, Adams. Foot small. The inferior (right) valve of the adult is perforated to admit of the passage of the byssus. Genera —*Anomia*, Linnaeus; byssus large and calcified; British. *Placuna*, Bruguière; byssus atrophied in the adult. *Hypotrema*, d'Orbigny. *Carolia*, Cantraine. *Ephippium*, Bolten. *Placunanomia*, Broderip.

SUB-ORDER 2. ARCACEA.

Symmetrical animals, with the mantle open throughout its extent, and with generally well-developed anterior and posterior adductor muscles. The heart lies in the pericardium and gives off two aortae. The gills are free and without interlamellar junctions. The renal and genital orifices are separate.

FAMILY 1. ARCIDAE, Gray. The borders of the mantle bear compound pallial eyes. The labial palps are direct continuations of the lips (Fig. 199). The hinge is "pliodont," that is to say, it has numerous teeth on either side of the umbones, and the teeth are perpendicular to the edge. Genera—*Arca*, Linnaeus ; foot byssiferous ; heart above the rectum ; hinge straight (Figs. 188, 199) ; British. *Pectunculus*, Lamarck ; foot without byssus, but with a plantar surface ; the heart traversed by the rectum ; the hinge curved ; British (Fig. 193, A). *Scaphula*, Benson ; from fresh water ; India. *Argina*, Gray. *Bathyarca*, Kobelt. *Barbatia*, Gray. *Senilia*, Gray. *Anadara*, Gray. *Adacnarca*, Pelseneer. FAMILY 2. PARALLELODONTIDAE, Dall. The shell of *Arca*, but with the posterior hinge teeth elongated and parallel to the cardinal border. Genera—*Cucullaea*, Lamarck ; recent and fossil from the Jurassic. All the other genera are fossil, *e.g. Parallelodon*, Meek and Worthen ; from the Devonian to the Tertiary. *Carbonaria*, Meek and Worthen ; from the Carboniferous, etc. FAMILY 3. LIMOPSIDAE, Dall. Shell sub-orbicular, the hinge curved, the ligament simple with the transverse axis longer than the longitudinal ; foot elongate, pointed anteriorly and posteriorly. Genera—*Limopsis*, Sassi ; shell covered with a hairy epidermis ; the anterior adductor frequently much reduced (Fig. 233). *Trinacria*, Mayer ; from the Tertiary. FAMILY 4. PHILOBRYIDAE, Bernard. The animal, like that of *Limopsis*, without an anterior adductor muscle ; the shell thin, very inequilateral, the anterior part atrophied, the umbones projecting and formed by the prodissoconch. Genera—*Philobrya*, Carpenter (Figs. 196, 234). FAMILY 5. CYRTODONTIDAE, Wöhrmann. An extinct family with an equivalve short, convex and inequilateral shell, the anterior side of which is short ; the hinge teeth oblique or horizontal. Genera — *Cyrtodonta*, Billings ; Silurian and Devonian. *Cypricardites*, Conrad ; Silurian. *Vanuxemia*, Billings ; Silurian. FAMILY 6. TRIGONIIDAE, Fleming. Foot elongated, pointed in front and behind, the ventral border sharp. The byssogenous apparatus atrophied and devoid of a byssus. The labial palps distinct from the lips. Shell thick. Hinge with striated teeth. Genera—*Trigonia*, Bruguière ; shell sub-triangular, the umbones directed back-

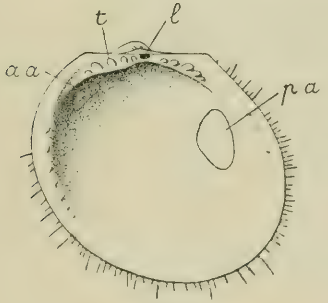

FIG. 233.

Limopsis longipilosa, Pels., interior aspect of the right valve. *a.a*, anterior adductor impression ; *l*, ligamentar fossa ; *p.a*, posterior adductor impression ; *t*, hinge-tooth.

wards. This genus was very abundant in the Secondary epoch, particularly in Jurassic seas. There are six living species, all of which live in Australian seas. The animal of *Trigonia* was first found by Quoy and Gaimard in 1827. *Schizodus*, King ; from the Permian. *Myophoria*, Bronn ; from the Trias. FAMILY 7. LYRODESMIDAE, Ulrich. Shell inequilateral, the posterior side being the shorter. The hinge short, bearing teeth disposed in the shape of a fan. An extinct family, from the Silurian. Genus — *Lyrodesma*, Conrad.

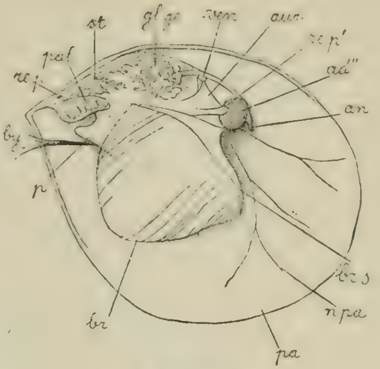

FIG. 234.

Philobrya sublaevis, Pels., viewed from the left side ; the left pallial lobe removed. *ad''*, posterior adductor muscle ; *an*, anus ; *au*, auricle of the heart ; *br*, gill ; *br.s*, branchial axis ; *by*, byssus ; *gl.ge*, gonad ; *n.pa*, pallial nerve ; *p*, foot ; *pa*, mantle ; *pal*, labial palp ; *re.p*, *re.p'*, anterior and posterior retractor muscles of the foot ; *st*, stomach ; *ven*, ventricle of the heart.

SUB-ORDER 3. MYTILACEA.

Symmetrical Lamellibranchia in which the anterior adductor muscle is always less developed than the posterior (the "anisomyarian" condition) or is absent (Fig. 193, B, C, D, E). The heart gives off a single vessel only, the anterior aorta. The gills are smooth, the gill-filaments all alike and provided with interlamellar junctions. The gonads generally extend into the mantle and open at the sides of the kidneys. The foot is linguiform and byssiferous.

FAMILY 1. MYTILIDAE, d'Orbigny. Shell inequilateral, the anterior side being short ; the hinge without teeth ; the ligament external. The mantle has a posterior suture. Cephalic eyes present. Genera—*Mytilus*, Linnaeus ; the shell with terminal umbones ; British. *Modiola*, Lamarck ; the umbones behind the anterior extremity ; British. *Lithodomus*, Cuvier ; the shell sub-cylindrical, adapted to boring. *Modiolaria*, Loven ; posterior pallial orifice provided with an elongated siphon ; anterior adductor fairly high ; British. *Crenella*, Brown. *Stavelia*, Gray. *Dacrydium*, Torell. *Myrina*, Adams. *Idas*, Jeffreys. *Septifer*, Recluz. FAMILY 2. MODIOLOPSIDAE, Fischer. Shell elongate, thin, inequilateral, enlarged posteriorly ; the ligament external ; the adductor muscles subequal. An extinct family from the Silurian to the Cretaceous. Genera—*Modiolopsis*, Hall ; from the Silurian. *Modiomorpha*, Hall ; from the Devonian. *Myoconcha*, Sowerby ; from the Carboniferous to the Cretaceous. FAMILY 3. PERNIDAE, Fleming. Mantle open throughout. No anterior adductor muscle. Shell very inequilateral ; the ligament multiple and lodged in a series of vertical fossae. Genera—*Perna*, Bruguière. Shell sub-quadrangular, the right valve notched for the passage of the byssus ; gills free posteriorly. *Crenatula*, Lamarck ; shell thin, flattened, irregular, without a byssal notch ; inhabits sponges. *Bakewellia*, King ; fossil from the Permian. *Gervilleia*, Defrance ; fossil from the Trias to the Eocene.

Odontoperna, Frech ; fossil from the Trias. *Inoceramus*, Sowerby ; fossil from the Jurassic to the Cretaceous.

SUB-ORDER 4. PECTINACEA.

Lamellibranchia with an open mantle and devoid of an anterior adductor muscle. The gills are folded, and the filaments at the summits and bottoms of the folds are different from the others. The gonads are contained in the visceral mass and generally open into the kidneys. Foot usually rudimentary.

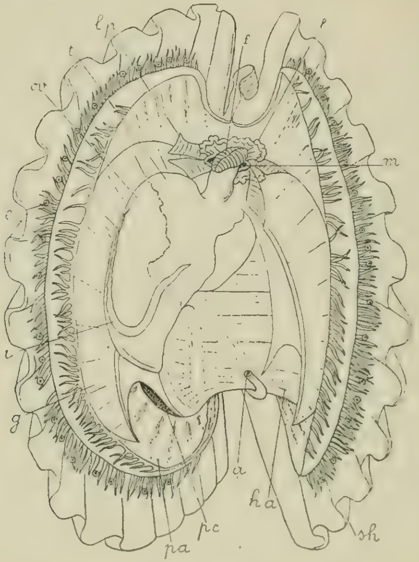

FIG. 235.

Pecten jacobaeus, ventral aspect. *a*, anus ; *e*, pallial eyes ; *f*, foot ; *g*, gill ; *h.a*, posterior adductor ; *i*, intestine ; *l*, lips ; *l.p*, labial palps ; *m*, mouth ; *ov*, ovary ; *pa*, mantle (reflected edge) ; *p.c*, pallial cavity ; *sh*, shell ; *t*, testis. (After Poli.)

FAMILY 1. VULSELLIDAE, Adams. Mantle open ; foot without byssus ; the shell high and the hinge without teeth. Genus—*Vulsella*, Lamarck. FAMILY 2. AVICULIDAE, Swainson. Foot provided with a very stout byssus (Fig. 236). The gills fused to the mantle ; shell very inequilateral ; the cardinal border straight, provided with two auriculae, of which the posterior is the longer. Genera—*Avicula*, Bruguière ; the auriculae of the shell very prominent ; heart attached to the ventral face of the rectum ; British ; fossil from the Devonian to the present day. *Meleagrina*, Lamarck ; shell sub-quadrangular, the auriculae not very prominent. A species of this genus, *Meleagrina margaritifera*, from the Indian Ocean, Persian Gulf, etc., forms precious pearls. *Malleus*, Lamarck ; shell irregular, high and narrow, with broad subequal auriculae. The following genera are exclusively fossil :—*Limopteria*, Hall; Devonian and Carboniferous. *Pseudomonotis*, Beyrick; Devonian and Cretaceous. *Cassianella*, Beyrich; Trias. *Monotis*, Bronn; Trias. *Daonella*, Mojsisovics; Trias. *Posidonomya*, Bronn; Silurian to Jurassic. FAMILY 3. PRASINIDAE, Stoliczka. Shell inequilateral with anterior umbones, and a prominent anterior auricula; the dorsal border arched; the hinge with a single fossa and a single tubercule on each valve. Genus—*Prasina*, Deshayes. FAMILY 4. PTERINEIDAE, Goldfuss. Shell thick, very inequilateral; the cardinal border straight, with two auriculae and a notch for the byssus under the right anterior auricula; an extinct family from the Palaeozoic. Genera—*Pterinea*, Goldfuss; Silurian to Carboniferous. *Rhombopteria*, Jackson; Silurian. *Actinodesma*, Sandberger; Devonian. FAMILY 5. LUNULICARDIIDAE, Fischer. Shell thin, triangular, very inequilateral, the anterior end truncated; the umbones terminal; the cardinal border straight; without hinge teeth. An extinct family from the Silurian and Devonian. Genera—*Lunulicardium*, Münster; Silurian and Devonian. *Patrocardium*, Fischer; Silurian. *Babinka*, Barrande; Silurian. FAMILY 6. CONOCARDIIDAE, Neumayr. Shell thick, subtriangular, the anterior side truncated and gaping; cardinal border straight and prolonged into two auriculae of which the anterior is very long and narrow; hinge with a lateral tooth and a reduced cardinal tooth. Dimyarian. An extinct family from the Palaeozoic. Genus—*Conocardium*, Bronn; Silurian to Carboniferous. FAMILY 7. AMBONYCHIIDAE, Miller. Shell inequilateral, without an anterior auricula, the umbones anterior and terminal; hinge with two

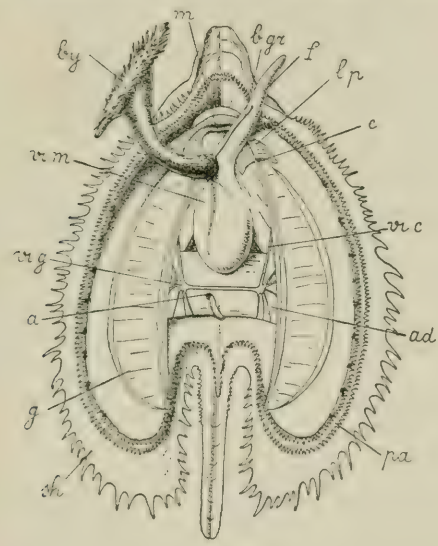

FIG 236.

Avicula tarentina, Lamarck, from below. *a*, anus; *ad*, adductor muscle; *b.gr*, byssal groove of the foot; *by*, byssus; *c*, eye; *f*, foot; *g*, gill; *l.p*, labial palp; *m*, mouth; *pa*, mantle; *sh*, shell; *vi.c*, visceral commissure; *vi.g*, visceral ganglion. (After Poli.)

cardinal teeth and two posterior oblique lateral teeth. Dimyarian, the anterior adductor being very small. An extinct family from the Silurian and Devonian. Genera—*Ambonychia*, Hall; Silurian. *Byssonychia*, Ulrich; Silurian. *Gosseletia*, Barrois; Devonian. *Clionychia*, Ulrich; Silurian. FAMILY 8. MYALINIDAE, Frech. Shell very inequilateral, the posterior part greatly enlarged; the umbones anterior or terminal; the hinge straight, without teeth; adductors subequal. An extinct family from the Silurian to the Cretaceous. Genera—*Myalina*, de Koninck; Silurian and Devonian. *Hoplomytilus*, Sandberger; Devonian. *Ptychodesma*, Hall; Devonian. *Anthracoptera*, Salter; Carboniferous. *Pergamidea*, Bittner; Trias. *Mysidea*, Bittner; Trias. *Aucella*, Kyser; Jurassic and Cretaceous. FAMILY 9. AMUSSIIDAE, Ridewood. Gills without interlamellar junctions. Shell orbicular, smooth externally, with radiating costae internally. Genus—*Amussium*, Klein. FAMILY 10. SPONDYLIDAE, Fleming. Shell very inequivalve, fixed by the right valve, which is larger than the left. The ligament elongated in a transverse direction. No byssus. Genera—*Spondylus*, Linnaeus; shell with spiny ribs, and adherent by the spines. *Plicatula*, Lamarck; shell folded, adherent by the umbo of the right valve. FAMILY 11. PECTINIDAE, Lamarck. Shell ornamented with radiating ribs; the dorsal border provided with two auriculae. Foot byssiferous. Mantle borders provided with eyes (Fig. 235). Genera—*Pecten*, Lamarck; shell orbicular, with equal auriculae; without a byssal sinus; British. *Chlamys*, Bolten; shell higher than it is long; the anterior auricula the larger, and provided with a byssal sinus; British. *Pedum*, Bruguière. *Hinnites*, Defrance. *Pseudamussium*, Adams. *Camptonectes*, Agassiz. *Hyalopecten*, Verrill; abyssal.

SUB-ORDER 5. DIMYACEA.

Dimyarian Lamellibranchia with an orbicular and almost equilateral shell; adherent; the hinge without teeth and the ligament internal. Gills with free non-reflected filaments.

Family DIMYIDAE, Dall; with the characters of the sub-order. Genus—*Dimya*, Ronault; recent, in abyssal depths, and fossil since the Jurassic.

ORDER 3. **Eulamellibranchia.**

Lamellibranchia in which the edges of the mantle are generally united by one or two sutures (Figs. 221, 241, etc.). Two adductor muscles are usually present (Figs. 238, 241, 242, etc.). In the gills the branchial filaments are united at regular intervals by vascular junctions which transform the linear interfilamentar spaces into a series of fenestrae (Fig. 237). Similarly the lamellae of each gill-plate have vascular junctions which form afferent vessels in the interior of the plates. The gonads always have their own proper external orifices. The order comprises the following nine sub-orders:—Ostraeacea, Submytilacea, Tellinacea, Veneracea, Cardiacea, Chamacea, Myacea, Adesmacea, Anatinacea.

Sub-Order 1. Ostraeacea.

Monomyarian Eulamellibranchia, or with a very small anterior adductor muscle. The mantle is open; the foot rather small; the branchiae folded; the shell inequivalve.

Family 1. Limidae, D'Orbigny. Foot digitiform, with a byssogenous apparatus. Borders of the mantle provided with long and numerous tentacles. Gills not united with the mantle. Shell provided with auriculae. Genera—*Lima*, Bruguière; the individuals of this genus form a sort of nest by means of the byssus, or swim by clapping the valves of the shell together. *Limaea*, Bronn. Family 2. Ostreidae, Gray. Foot much reduced and devoid of a byssus. Heart generally on the ventral side of the rectum. The gills fused to the mantle. Shell irregular, fixed by the left and larger valve. Genera—*Ostraea*, Linnaeus; foot absent in the adult; eatable and cultivated for commerce; some species, such as the British *O. edulis*, are hermaphrodite. Family 3. Eligmidae, Gill. Shell thick, inequilateral, the anterior side being the shorter. Monomyarian, with the muscular impression on a prominent myophorous apophysis. Genus—*Eligmus*, Deslongchamps; an extinct genus from the Jurassic. Family 4. Pinnidae, Meek. Shell elongated. Dimyarian, with a very small anterior adductor

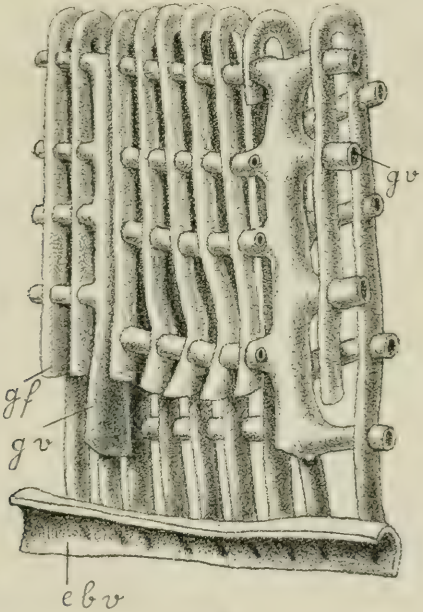

Fig. 237.

A portion of the gill of *Venus*. *e.b.v*, efferent branchial vessel; *g.f*, gill filaments; *g.v*, afferent branchial vessels. (After Bonnet.)

muscle. Shell truncated and gaping posteriorly. Foot byssiferous. Genera—*Pinna*, Linnaeus; heart traversed by the intestine; anus projecting and appendiculated. *Cyrtopinna*, Mörch. *Aviculopinna*, Meek; fossil from the Carboniferous and Permian. *Pinnigena*, de Saussure; fossil from the Jurassic and Cretaceous. *Atrina*, Gray; from the Carboniferous to the present day.

SUB-ORDER 2. SUBMYTILACEA.

Eulamellibranchia in which the mantle is only slightly closed; generally there is only a single suture. Siphons absent or very short. Gills smooth. Nearly always dimyarian. Shell equivalve, with an external ligament.

FAMILY 1. DREISSENSIIDAE, Gray. Two pallial sutures and two short siphons; pedal orifice short. Foot cylindrical with a stout byssus. Shell elongated; the hinge without teeth; the summits of the valves with an internal septum. Genus—*Dreissensia*, van Beneden; an inhabitant of fresh water, but originated from the Caspian Sea; acclimatised in England about 1824. FAMILY 2. MODIOLARCIDAE, Gray. Mantle with two sutures. The foot byssiferous, with a plantar surface and a glandular cavity in front of the byssogenous cavity. The two branchial plates serve as incubatory pouches. Genus—*Modiolarca*, Gray; subantarctic (Fig. 241). FAMILY 3. ASTARTIDAE, d'Orbigny. A single pallial suture. Foot elongate, without a byssus. Shell concentrically striated; the ligament external. Genera—*Astarte*. Sowerby; British. *Woodia*, Deshayes. *Opis*, Defrance; fossil from the Secondary. *Prosocoelus*, Keferstein; fossil from the Devonian. FAMILY 4. CRASSATELLIDAE, Gray. Mantle with a single suture; foot short. Shell thick with concentric striae; the ligament external. Genera—*Crassatella*, Lamarck. *Cuna*, Hedley. FAMILY 5. CARDITIDAE, Férussac. Mantle with a single pallial suture; foot carinated, often byssiferous; palps short. Shell thick with radiating costae; the ligament external. Genera—*Cardita*, Bruguière. *Thecalia*, Adams. *Milneria*, Dall; incubatory, California. *Venericardia*, Lamarck. FAMILY 6. CONDYLOCARDIIDAE, Bernard. Distinguished from the family Carditidae by the presence of an external ligament. Genera—*Condylocardia*, Bernard. *Carditella*, Smith. *Carditopsis*, Smith. FAMILY 7. CYPRINIDAE, d'Orbigny. Mantle open in front, and with two pallial sutures. The branchial and anal orifices papillose, the latter projecting. External gill-plates smaller than the internal. Genera—*Cyprina*, Lamarck; British. *Cypricardia*, Lamarck. *Coralliophaga*, de Blainville. *Pleurophorus*, King; fossil from the Devonian to the Trias. *Anisocardia*, Munier-Chalmas; fossil from the Jurassic to the Tertiary. *Veniella*, Stoliczka; fossil from the Cretaceous to the Tertiary. FAMILY 8. ISOCARDIIDAE, Gray. Mantle largely closed, the pedal orifice generally small; the anal and branchial orifices sessile; gill-plates of equal size; foot short. Shell globular with prominent and coiled umbones. Genus—*Isocardia*, Lamarck; British. FAMILY 9. CALLOCARDIIDAE, Dall. The anal and branchial orifices of the mantle provided with siphons. The external gill-plate smaller than the internal. Shell ventricose, but elongated; the umbones not prominent. Genus—*Callocardia*, Adams; abyssal. FAMILY 10. LUCINIDAE, d'Orbigny. The anal orifice of the mantle sometimes produced into a siphon. Anterior adductor muscle within the pallial line. Labial palps very small. Gills without an external plate. Shell rather thin. Genera—*Lucina*, Bruguière; mantle with two sutures; visceral mass smooth; foot vermiform; British. *Montacuta*, Turton; shell with a single suture, foot short, byssiferous; visceral mass with arborescent projections; British. *Cryptodon*, Turton; mantle with a single aperture; foot short; visceral mass smooth. FAMILY 11. CORBIDAE, Dall. Shell thick with denticulated borders. The anal orifice provided with a valve, but not with a siphon. Foot elongated and pointed. Genera — *Corbis*, Cuvier. *Gonodon*, Schafhäutl; fossil from the Trias and Jurassic. *Mutiella*, Stoliczka; fossil from the superior Cretaceous. FAMILY 12. UNGULINIDAE, Adams. Mantle without siphons; the pedal orifice long. Foot greatly elongated, vermiform, ending in a glandular enlargement (Fig. 238, III). Anterior adductor muscle in contact with the pallial line. Gills with two plates; labial palps small. Marine. Genera — *Ungulina*, Daudin; mantle with a single suture; visceral mass smooth. *Diplodonta*, Bronn; mantle with two sutures; British. *Axinus*, Sowerby; mantle with a single suture; visceral mass with arborescent excrescences (Fig. 238); British. FAMILY 13. CYRENELLIDAE, Fischer. Mantle provided with two elongated, united, non-retractile siphons. Two gill-plates to each gill; labial palps elongated. Inhabitants of fresh water. Genera—*Cyrenella*, Deshayes. *Joanisiella*, Dall. FAMILY 14. TANCREDIIDAE, Fischer. Shell elongate, sub-triangular; the ligament external. Hinge with two cardinal teeth on the right and one or two on the left valve. Posterior lateral teeth stout. An extinct family ranging from the Trias to the Cretaceous. Genera—*Tancredia*, Lycett; Trias to Cretaceous. *Meekia*, Gabb; Cretaceous. FAMILY 15. UNICARDIIDAE, Fischer. Shell sub-orbicular, more or less ventricose, nearly equilateral, with concentric striae; pallial line simple; hinge with a single cardinal tooth on each valve. An extinct family ranging from the Carboniferous to the Cretaceous. Genera—*Unicardium*, d'Orbigny; Trias to Cretaceous. *Scaldia*, de Ryckholt; Carboniferous. *Pseudedmondia*, Fischer; Carboniferous. FAMILY 16. LEPTONIDAE, Gray. Shell thin, not covered by the mantle and not gaping. Mantle without siphons; gills with two gill-plates; foot long and byssiferous. Marine, hermaphrodite and incubatory animals.

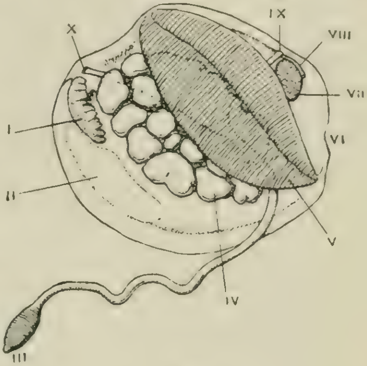

FIG. 238.

Axinus flexuosus, Montagu, viewed from the left side. I, anterior adductor muscle; II, glandular portion of the mantle; III, foot; IV, gonad projecting into the pallial cavity; V, internal plate of the gill; VII, posterior adductor muscle; VIII, rectum; IX, posterior retractor of the foot; X, anterior retractor of the foot.

Genera—*Kellya*, Turton ; mantle with two sutures and three orifices, the pedal orifice being the middle and not the anterior of the three (Fig. 187) ; foot linguiform ; the external gill-plate with a reflected lamella ; British. *Lepton*, Turton; mantle with a single suture ; the mantle edges provided with tentacles ; foot with a plantar ventral surface ; commensal ; British. *Lasaea*, Leach ; a single pallial suture ; the foot linguiform and elongated ; the external gill-plate not reflected (Fig. 206, G) ; British. *Erycina*, Lamarck ; fossil from the Tertiary. *Pythina*, Hinds. *Scacchia*, Philippi. *Sportella*, Deshayes. *Cyamium*, Philippi. FAMILY 17. GALEOMMIDAE, Gray. Mantle more or less completely reflected over the shell. Foot well developed, generally byssiferous. Shell thin, gaping ; the adductor muscles much reduced. Genera—*Galeomma*, Turton ; shell incompletely covered by the mantle ; a single pallial suture ; a large azygos anterior pallial tentacle, and a short anal siphon present. A byssal groove in the foot ; British. *Scintilla*, Deshayes. *Hindsiella*, Stoliczka. *Ephippodonta*, Tate ; shell internal ; a single pallial suture ; gills with two gill-plates ; commensal with the shrimp *Axius ;* Australian. The three following genera with an internal shell probably belong to this family :—*Chlamydoconcha*, Dall ; two gill-plates ; a pallial suture ; an anterior orifice leading into a caecum ; no adductor muscles ; sexes separate ; from California (Fig. 239). *Scioberetia*, Bernard ; gills with a single gill-plate ; a single pallial suture ; foot large, elongated, with a byssal groove ; hermaphrodite and commensal with a Spatangid, *Triphylus* ; from Cape Horn. *Entovalva*, Voeltzkow (Fig. 240) ; mantle fairly open, with a single suture ; foot large, with a posterior pore ; hermaphrodite and incubatory ; endoparasitic in *Synapta* (= *Synapticola*, Malard), Madagascar and Atlantic. FAMILY 18. KELLYELLIDAE, Fischer. Mantle with a single pallial suture ; anal orifice with a very short siphon ; foot elongated ; gills with two unequal plates. Shell ovoid ; the ligament external ; the anterior lateral hinge tooth below the cardinal tooth. Genera — *Kellyella*, Sars. *Turtonia*, Forbes and Hanley ; British. *Allopagus*, Stoliczka ; fossil from the Eocene. *Lutetia*, Deshayes ; fossil from the Eocene. FAMILY 19. CYRENIDAE, Gray. Mantle with two siphons, which are more or less intimately united together and have papillose orifices. The sexes separate. Shell with external ligament; the pallial line usually with a sinus. Freshwater forms. Genera—*Cyrena*, Lamarck. *Corbicula*, Megerle. *Batissa*, Gray. *Velorita*, Gray. *Galatea*, Bruguière. *Fischeria*, Bernardi. FAMILY 20.

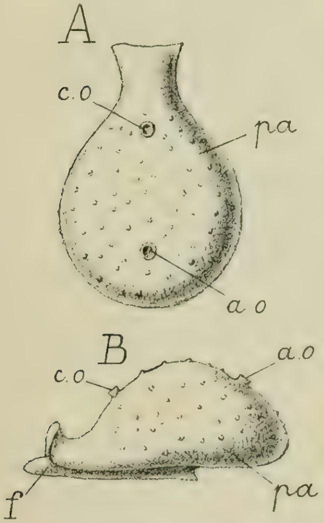

FIG. 239.

Chlamydoconcha orcutti, Dall. *A*, dorsal aspect ; *B*, left-side view. *a.o*, anal orifice ; *c.o*, caecal orifice ; *f*, foot ; *pa*, mantle. (After Bernard.)

Cycladidae, Clark. Mantle with one siphon or with two free siphons, which have simple orifices. Hermaphrodite; the embryos incubated in the external gill-plate. Shell with a simple pallial line. Freshwater. Genera—*Cyclas*, Bruguière (= *Sphaerium*); two siphons; British (Fig. 218). *Pisidium*, Pfeiffer; a single anal siphon; British. Family 21. Rangiidae. Mantle with two short siphons united at their bases, and with papillose orifices. Foot linguiform. Shell with prominent umbones and an internal ligament. Genus—*Rangia*, Desmoulins; from brackish water in Florida. Family 22. Cardiniidae, Zittel. Shell elongated, inequilateral, the posterior side being the longer; the ligament external; the pallial line simple; dimyarian. An extinct family, ranging from the Devonian to the Cretaceous. Genera—*Cardinia*, Agassiz; Trias and Jurassic. *Anthracosia*, King; Carboniferous and Permian. *Anoplophora*, Sandberger; Trias. *Pachycardia*, Hauer; Trias. Family 23. Megalodontidae, Zittel. Shell inequilateral, thick, dimyarian, with prominent umbones; the posterior adductor impression borne on a myophorous apophysis. An extinct family, ranging from the Devonian to the Cretaceous. Genera—*Megalodon*, Sowerby; from the Devonian to the Jurassic. *Pachyrisma*, Morris and Lycett; Trias and Jurassic. *Durga*, Böhm; Jurassic. *Dicerocardium*, Stoppani; Jurassic. Family 24. Unionidae, Fleming. Mantle with a single pallial suture and no siphons. Shell equilateral, with lateral hinge teeth or no hinge teeth. Inhabitants of fresh water. Development through a glochidium

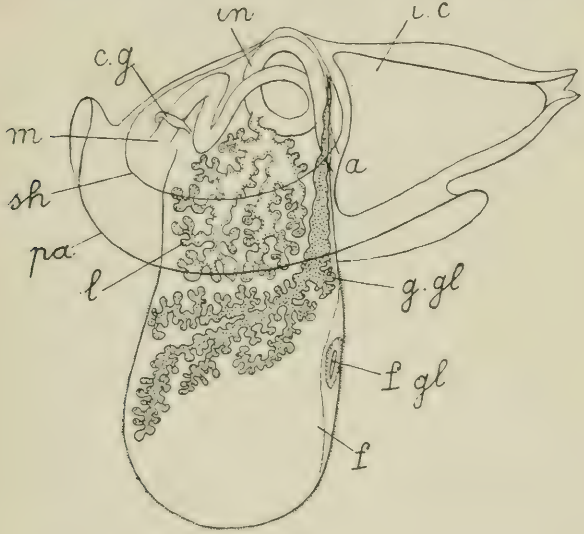

Fig. 240.

Entovalva, left-side view. *a*, anus; *c.g*, cerebral ganglion; *f.gl*, foot-gland; *g.gl*, gonad; *i.c*, incubatory chamber; *in*, intestine; *l*, liver; *m*, mouth; *pa*, mantle; *sh*, shell. (After Voeltzkow.)

stage (Fig. 242). Genera—*Unio*, Retzius; shell thick, the hinge toothed. This genus includes more than a thousand species, the majority from the northern hemisphere. *Anodonta*, Lamarck; shell thin; the hinge without teeth; British. *Pseudodon*, Gould. *Quadrula*, Rafinesque. *Arconaia*, Conrad. *Monocondylaea*, d'Orbigny. *Solenaia*, Conrad. *Mycetopus*, d'Orbigny; foot cylindrical, with a terminal swelling; South America. FAMILY 25. MUTELIDAE, Gray. This family differs from the Unionidae in having two pallial sutures and a distinct branchial orifice; the shell is never furnished with lateral hinge teeth. Freshwater. Genera—*Mutela*, Scopoli. *Pliodon*, Conrad. *Spatha*, Lea. *Iridina*, Lamarck. *Hyria*, Lamarck. *Castalia*, Lamarck. *Aplodon*, Spix. *Plagiodon*, Spix. FAMILY 26. AETHERIIDAE, Adams. Shell irregular, generally fixed in the adult state. Mantle with a single suture; foot absent; anterior adductor muscle sometimes reduced or absent; from fresh water. Genera—*Aetheria*, Lamarck; anterior adductor well developed; African. *Mülleria*, Férussac; no anterior adductor; American. *Bartlettia*, Adams.

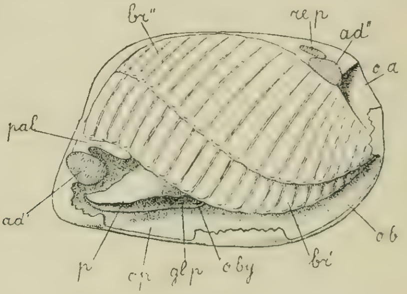

FIG. 241.

Modiolaria trapezina, Lamarck, viewed from the left side; the left mantle lobe is removed. *ad'*, *ad''*, anterior and posterior adductor muscles; *br'*, *br''*, internal and external gill-plates; *gl.p*, foot gland; *o.a*, *o.b*, anal and branchial orifices of the mantle; *o.by*, byssal orifice of the foot; *o.p*, pedal orifice of the mantle; *p*, foot; *pal*, labial palp; *re.p*, posterior retractor muscle of the foot.

SUB-ORDER 3. TELLINACEA.

Eulamellibranchia in which the mantle is not extensively closed, with two pallial sutures and two well-developed siphons; the gills smooth. The foot is compressed and elongated. The labial palps very large. Dimyarian; the pallial line has a deep sinus.

FAMILY 1. TELLINIDAE, Deshayes. The external branchial plate directed upwards (Fig. 206, H). The siphons separate and elongated. Foot with a byssogenous apparatus. Palps very large. Ligament of shell external. Genera—*Tellina*, Linnaeus; slightly inequivalve; foot large; British (Fig. 190). *Gastrana*, Schumacher; equivalve; the foot slightly developed; British. *Capsa*, Bruguière. *Macoma*, Leach. FAMILY 2. SCROBICULARIIDAE, Adams. External gill-plate directed upwards. Siphons separate and excessively long. Foot without a byssus. The ligament partly internal, lodged in a concavity in the hinge. Genera—

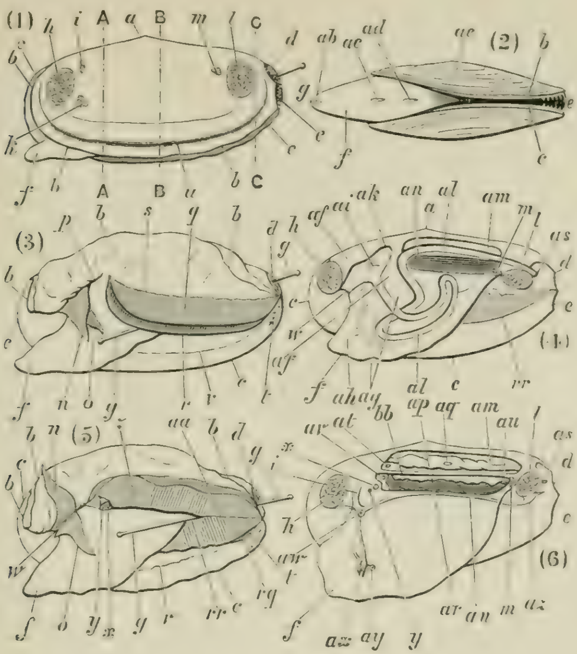

Fig. 242.

Diagrams of the external form and anatomy of *Anodonta cygnaea* (2), ventral view, all the other figures seen from the left side. (1) animal removed from its shell; a probe *g* passed into the infra-branchial chamber through the excurrent siphonal notch. (2) view from the ventral surface of *Anodonta*, with its foot expanded and issuing from between the gaping valves. (3) the left mantle-flap reflected upwards so as to expose the sides of the body. (4) diagrammatic sagittal section of *Anodonta* to show the course of the alimentary canal. (5) the two gill-plates of the left side reflected upwards, so as to expose the fissure between foot and gill where the probe *g* passes. (6) diagram to show the positions of the nerve ganglia, heart, and kidney. *a*, centro-dorsal area; *b*, margin of the left mantle-flap; *c*, margin of the right mantle-flap; *d*, excurrent (anal) siphonal notch of the mantle-margin; *e*, incurrent (branchial) siphonal notch; *f*, foot; *g*, probe passed into the superior division of the sub-pallial chamber through the anal siphonal notch, and issuing by the side of the foot into the infra-branchial chamber; *h*, anterior adductor muscle; *i*, anterior retractor muscle of the foot; *k*, protractor muscle of the foot; *l*, posterior adductor muscle; *m*, posterior retractor muscle of the foot; *n*, anterior labial palp; *o*, posterior labial palp; *p*, base-line of origin of the reflected mantle-flap from the side of the body; *q*, left external gill-plate; *r*, left internal gill-plate; *rr*, inner lamella of the right inner gill-plate; *r.g*, right outer gill-plate; *s*, line of concrescence of the outer lamella of the left outer gill-plate with the left mantle-flap; *t*, pallial tentacles; *u*, the thickened muscular pallial margin which adheres to the shell and forms the pallial line of the left side; *v*, that of the left side; *w*, the mouth; *x*, aperture of the left kidney, exposed by cutting the attachment of the inner lamella of the inner gill-plate; *y*, aperture of the genital duct; *z*, fissure between the free edge of the inner lamella of the inner gill-plate and the side of the foot, through which the probe *g* passes into the supra-branchial chamber; *aa*, line of concrescence of the inner lamella of the right inner gill-plate with the inner lamella of the left inner gill-plate; *ab*, *ac*, *ad*, three pit-like glandular depressions in the median line of the foot; *ae*, left shell-valve; *af*, space occupied by the liver; *ag*, space occupied by the gonad; *ah*, muscular substance of the foot; *ai*, opening of bile-duct into the stomach; *ak*, stomach; *al*, rectum traversing the ventricle of the heart; *am*, pericardium; *an*, glandular portion of the left kidney; *ap*, ventricle of the heart; *aq*, auriculo-ventricular orifice; *ar*, non-glandular portion of the left kidney; *as*, anus; *at*, reno-pericardial orifice; *au*, pore joining the two parts of the kidney; *av*, internal pore of the kidney leading to the external pore *x*; *aw*, left cerebral ganglion; *ax*, left pedal ganglion; *ay*, left otocyst; *az*, left visceral ganglion; *bb*, floor of the pericardium, separating that space from the kidney. (After Lankester.)

Scrobicularia, Schumacher; estuarine; British. *Syndosmya*, Recluz; British. *Cumingia*, Sowerby. Family 3. Donacidae, Fleming. External gill-plate directed ventrally. Siphons separate, of moderate length, the anal siphon being the longer. Foot large and compressed. Shell inequilateral, the anterior side being the longer; the ligament external. Genera—*Donax*, Linnaeus; British. *Iphigeneia*, Schumacher. Family 4. Mesodesmatidae, Deshayes. External branchial plate directed ventrally. Siphons separate and equal. Shell inequilateral, the anterior side being the longer; ligament internal. Genera—*Mesodesma*, Deshayes. *Ervilia*, Turton; British. Family 5. Cardiliidae, Dall. Shell very high and short, ventricose, dimyarian, the posterior adductor impression borne on a prominent myophorous apophysis. Ligament partly internal. Genus—*Cardilia*, Deshayes; from the Pacific Ocean. Family 6. Mactridae, Gray. External branchial plate directed ventrally. Siphons united, more or less invested by a chitinous sheath. Foot long, stout, bent at an angle and without a byssus. Shell subtriangular and nearly equilateral; the ligament partly internal. Genera—*Mactra*, Linnaeus; British (Fig. 191). *Mulinia*, Gray. *Harvella*, Gray. *Racta*, Gray. *Eastonia*, Gray. *Heterocardia*, Deshayes. *Vanganella*, Gray.

Sub-Order 4. Veneracea.

Eulamellibranchia with two pallial sutures; the siphons generally somewhat elongated and partially or wholly united. Gills slightly folded. A bulb on the posterior aorta. Ligament external.

Family 1. Veneridae, Gray. Foot well developed. Adductor muscles subequal. Pallial sinus shallow or absent. Genera—*Venus*, Linnaeus; siphons rather short, their distal extremities free; foot without byssus; British. *Dosinia*, Scopoli; siphons long and fused together throughout their length; foot truncated without a byssus; British *Tapes*, Megerle; siphons rather long and incompletely fused; foot byssiferous; British (Fig. 202). *Cyclina*, Deshayes. *Lucinopsis*, Forbes and Hanley; British. *Meretrix*, Lamarck (Fig. 189). *Circe*, Schumacher; British. *Venerupis*, Lamarck. Family 2. Petricolidae, d'Orbigny. Boring Lamellibranchs with a reduced foot. The shell more or less elongated, with a deep pallial sinus. Genera—*Petricola*, Lamarck; the British species *P. pholadiformis*, originally an inhabitant of the United States, has been acclimatised for some years in the North Sea: it has boring habits as and mimics *Pholas candida*. Family 3. Glaucomyidae, Chenu. Siphons very long and united. Foot small. Shell elongated, thin, with a deep pallial sinus. Inhabitants of fresh or brackish water. Genera—*Glaucomya*, Woodward; from S.E. Asia. *Tanysiphon*, Benson; from India.

Sub-Order 5. Cardiacea.

Eulamellibranchia with two pallial sutures. Generally with short siphons. The foot cylindrical, more or less elongated, furnished with a byssogenous apparatus. The gills much folded. Shell equivalve, with radiating costae and an external ligament.

FAMILY 1. CARDIIDAE, Gray. The mantle slightly closed; siphons very short and surrounded by a single circle of papillae which are often oculiferous (Fig. 243, *o.t*). Foot very long, geniculated. Pallial line of the shell without a sinus; two adductor muscles. Genera—*Cardium*, Linnaeus; adductor muscles subequal; British (Fig. 243). *Pseudokellya*, Pelseneer (Fig. 221). Both *Byssocardium*, Munier-Chalmas, and *Lithocardium*, Woodward, fossils from the Eocene, have a much reduced anterior adductor muscle. FAMILY 2. LIMNOCARDIIDAE, Stoliczka. Siphons very long, united throughout their extent. Shell gaping; two adductor muscles. Inhabitants of brackish waters. Genera—*Adacna*, Eichwald; from the Caspian Sea. *Limnocardium*, Stoliczka; from the Caspian Sea and fossil from the Tertiary. *Arcicardium*, Fischer; fossil from the Tertiary. FAMILY 3. TRIDACNIDAE, Broderip. Mantle closed to a considerable extent, the orifices distant from one another; no siphons. The foot short, with a more or less well developed byssus. A single adductor muscle. The gills narrow. The shell thick. Genera—*Tridacna*, Bruguière; byssus stout; shell gaping anteriorly; from the Indian and Pacific Oceans. *Hippopus*, Lamarck; byssus reduced; shell not gaping.

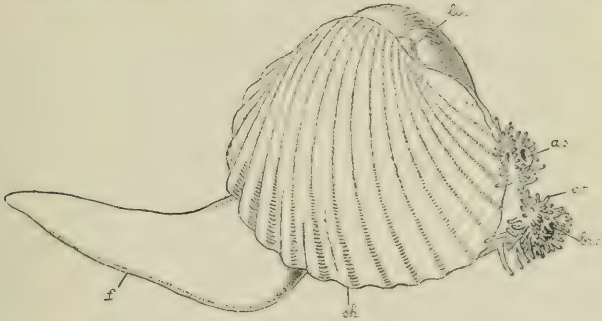

FIG. 243.

Cardium edule, left-side view. *a.s*, anal siphon; *br.s*, branchial siphon; *f*, foot; *li*, ligamen of the shell; *o.t*, eye-spots on the tentacles; *sh*, shell. (After Deshayes.)

SUB-ORDER 6. CHAMACEA.

Asymmetrical, inequivalve, fixed Eulamellibranchia, with extensive pallial sutures and distant pallial orifices; no siphons. Two adductor muscles present. The foot reduced and without a byssus. Shell thick, without a pallial sinus.

FAMILY 1. CHAMIDAE, Gray. Shell with subequal valves and prominent umbones more or less spirally coiled; ligament external. Genera—*Chama*, Bruguière; the free valve only slightly ventricose; shell lamellated or spiny. *Diceras*, Lamarck; shell smooth, the umbones largely divergent and coiled; the adductor muscles (at least the anterior) attached to myophorous apophyses; fossil from the Jurassic (Fig. 244, A). *Requienia*, Matheron; the fixed valve spirally coiled; the free valve operculiform; fossil from the Cretaceous (Fig. 244, B). *Matheronia*, Munier-Chalmas; fossil from the Cretaceous. FAMILY 2. CAPRINIDAE, d'Orbigny. Shell inequivalve; the fixed valve spiral or conical; the free valve not operculiform but coiled or spiral; ligament internal; substance of the shell generally pierced with large parallel canals. An exclusively fossil family, from the Cretaceous. Genera—*Caprina*, d'Orbigny; the free valve larger than the fixed and coiled (Fig. 244, C). *Caprinula*, d'Orbigny; fixed valve elongated and conical, free valve small and coiled (Fig. 244, D). *Caprotina*, d'Orbigny. *Ichthyosarcolites*, Desmarets. *Plagioptychus*, Matheron. *Polyconites*, Roulland. FAMILY 3. MONOPLEURIDAE, Munier-Chalmas. Shell very inequivalve; the fixed valve conical or spiral, the free valve operculiform and slightly or not at all spiral; ligament external. No canals in the substance of the shell. An exclusively fossil family, from the Cretaceous. Genera—*Monopleura*, Matheron (Fig. 244, E). *Valletia*, Munier-Chalmas. *Baylea*, Munier-Chalmas. The two following families, designated by the common name of *Rudistae*, are closely allied to the preceding: they also comprise some extinct marine forms from Secondary deposits. These animals, of littoral and often gregarious habit, were fixed by the conical and more or less elongated right valve; the adductor muscles were not inserted perpendicularly to the surface of separation of the two valves; the free left valve has a sub-central umbo, is not spiral, and is furnished with prominent myophorous apophyses to whose external faces the muscles were attached; this valve was only movable in a vertical direction. FAMILY 4. RADIOLITIDAE, Gray. Shell conical or biconvex, without canals in the external layer. Genera—*Radiolites*, Lamarck; valves ornamented with longitudinal costae; a ligament present; from the Cretaceous (Fig. 244, F). *Biradiolites*, d'Orbigny; no ligament; Cretaceous. FAMILY 5. HIPPURITIDAE, Gray. Fixed valve long, cylindro-conical, with three longitudinal furrows, corresponding internally to two pillars which serve to support the siphons. Anterior adductor muscle with two separate insertions on the fixed valve. Genera—*Hippurites*, Lamarck; Cretaceous. *Arnaudia*, Bayle; Cretaceous. The family Diceratidae, the most ancient

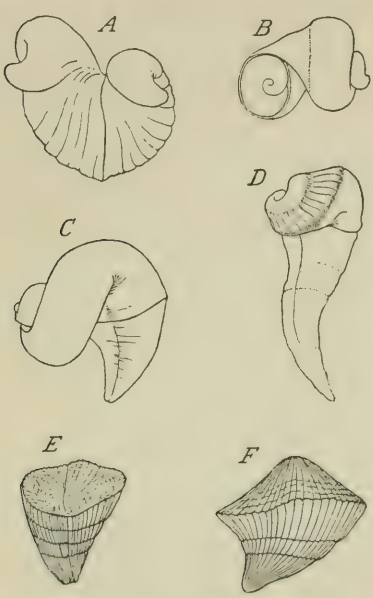

FIG. 244.

Some genera of fossil Chamacea and Rudistae. *A, Diceras arietinum; B, Requienia ammonia; C, Caprina adversa; D, Caprinula Baylei; E, Monopleura imbricata; F, Radiolites angeiodes.* (Chiefly after d'Orbigny.)

of the Chamacea, and possibly derived from the Megalodontidae of the Palaeozoic and the Trias, has given rise to a branch that has survived to the present epoch (Chamidae) and to various others that became extinct at the close of the Secondary period. In all cases, the forms in which the umbo of the free valve is coiled have preceded the forms with an operculiform free valve—*Requienia* being derived from *Diceras* and *Chama* from *Matheronia*; in the same way among the Rudistae *Radiolites* appears to be derived from *Caprina*. The Hippuritidae, by the depth of the fixed valve, the reduction of the cavity, and the absence of the ligament, indicate the last stage of the evolutionary series.

SUB-ORDER 7. MYACEA.

Eulamellibranchia in which the mantle is closed to a considerable extent; the siphons are well developed, the gills much folded and frequently prolonged into the branchial siphon. The foot is compressed and generally byssiferous. The shell gaping, with a pallial sinus.

FAMILY 1. PSAMMOBIIDAE, Gray. Siphons very long and quite separate. Foot large, flattened from side to side and pointed. Shell oval, elongated, with a deep pallial sinus and an external ligament. Genera—*Psammobia*, Lamarck; the posterior end of the shell subtruncated; British (Fig. 245). *Sanguinolaria*, Lamarck. *Asaphis*, Modeer. *Elizia*, Gray. *Solenotellina*, de Blainville. FAMILY 2. MYIDAE, Gray. Mantle largely closed; siphons united for the greater part of their length and surrounded, near their extremities, by a circlet of tentacles. Foot reduced. Shell gaping, with an internal ligament; the left valve provided with a spoon-shaped projection for the ligament. Genera—*Mya*, Linnaeus; siphons elongated, covered by a chitinous sheath, and incompletely retractile; foot small; palps elongated; British. *Sphenia*, Turton; British. *Tugonia*, Gray. *Platyodon*, Conrad. *Cryptomya*, Conrad. FAMILY 3. CORBULIDAE, Fleming. Shell sub-trigonal, inequivalve, the left valve less convex than the right; the pallial sinus shallow; the ligament partly external. Siphons short, united, completely retractile. Foot large, pointed, often byssiferous. Palps reduced. Genera—*Corbula*, Bruguière; siphons surrounded by a common circlet of tentacles; shell short; British. *Corbulomya*, Nyst; shell elongated; branchial siphon with a special tentacular crown. *Paramya*, Conrad. *Erodona*, Daudin, and *Himella*, Adams, are fluviatile forms from South America. FAMILY 4. LUTRARIIDAE, Adams. Mantle extensively

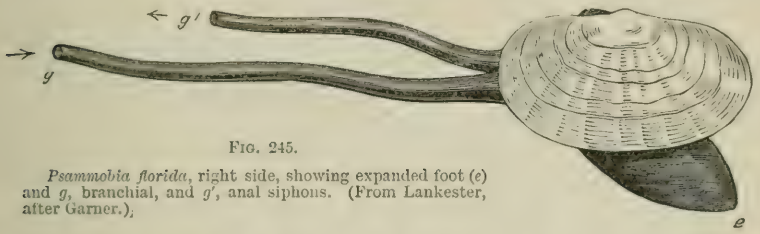

FIG. 245.

Psammobia florida, right side, showing expanded foot (*e*) and *g*, branchial, and *g′*, anal siphons. (From Lankester, after Garner.)

closed; siphons long and united throughout their length; a fourth opisthopodial pallial aperture. Foot rather large, compressed. Shell elongated, with a deep pallial sinus and a spoon-shaped projection for the ligament on each valve. Genera—*Lutraria*, Lamarck; British. *Tresus*, Gray. *Standella*, Gray. Family 5. Solenidae, Leach. Elongated, burrowing animals. The foot more or less cylindrical and powerful, without a byssus. Gills narrow. Shell long, truncated, and gaping at each end; the ligament external. Genera—*Solenocurtus*, de Blainville; siphons large, partially united, incompletely retractile; pallial sinus deep; foot very large and linguiform (Fig. 194); British. *Tagelus*, Gray; posterior extremity short; pallial sinus very deep; estuarine. *Ceratisolen*, Forbes and Hanley; siphons long, separate; gills rather short and not folded; British. *Cultellus*, Schumacher; siphons rather short; extremity of foot dilated; British. *Siliqua*, Megerle; siphons of medium length; foot dilated; shell compressed. *Solen*, Linnaeus; siphons short; foot elongated; shell rectilinear, cylindrical; the umbones anterior and terminal; British. *Ensis*, Schumacher; siphons very short; a fourth pallial orifice; shell arcuate, the umbones anterior and sub-terminal; British. Family 6. Saxicavidae, Gray. Mantle extensively closed; with a small pedal orifice (Fig. 246, *f*); siphons elongate, covered by a chitinous sheath and wholly or largely united; gills prolonged into the branchial siphon. Foot small. Shell gaping, with an external ligament. Genera—*Saxicava*, Fleuriau; bores holes in rocks; siphons free at their extremities; foot byssiferous; British (Fig. 246). *Glycimeris*, Lamarck; siphons very long and completely united; a burrowing form. *Cyrtodaria*, Daudin; shell inequilateral; the anterior side the longer; siphons united, incompletely retractile. Family 7. Gastrochaenidae, Gray. Shell thin, without teeth, gaping widely at the anterior end. Anterior adductor much reduced. Foot small and without a byssus. Gills narrow. Mantle extensively closed; with long united siphons. Genera—*Gastrochaena*, Spengler; a boring form, with a cylindrical foot; the shell regular and rarely enclosed in an adventitious tube; British. *Fistulana*, Bruguière; a burrowing form with a very small compressed foot; shell with a denticulate border, always enclosed in a regular, non-adherent, fragile, club-shaped adventitious tube.

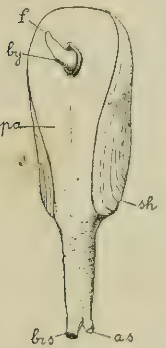

Fig. 246.

Saxicava arctica, ventral aspect. *a.s*, anal siphon; *br.s*, branchial siphon; *by*, byssal orifice; *f*, foot; *pa*, mantle; *sh*, shell.

Sub-Order 8. Adesmacea.

Eulamellibranchia with very long united siphons and a largely closed mantle. The foot short, truncated, discoid, and without a byssus. The gills prolonged into the branchial siphon. The shell gaping and devoid of a ligament, but with a styloid apophysis in the umbonal cavities.

Family 1. Pholadidae, Adams. Shell capable of containing all the organs; the heart traversed by the rectum; two aortae. The shell with a pallial sinus; the dorsal region protected by accessory calcareous pieces. Genera—*Pholas*, Linnaeus; foot cylindrical; siphons free near their extremities; British. In *Pholas* there are four accessory plates; in *Zirphaea*, Leach, two; in *Barnea*, Leach, one. *Pholadidea*, Goodall; foot rudimentary; siphons completely united and their extremity surrounded by a fringed disc; shells elongated, in the adult prolonged posteriorly by a short calcareous tube, which surrounds the siphons; British. *Jouannetia*, des Moulins; foot rudimentary; siphons completely united; shell globular, and the right valve prolonged posteriorly by a rostriform appendage. *Xylophaga*, Turton; siphons separate at their extremities; foot narrow; shell globular with two accessory dorsal plates; British. *Martesia*, Leach; siphons long, united; foot absent in the adult; shell ovoid with a ventral plate in addition to the dorsal plates. FAMILY 2. TEREDINIDAE, Fleming. Shell globular, covering a small portion only of the vermiform body. Heart on the ventral side of the rectum (Fig. 195, *h*); a single aorta; siphons long, united to a large extent and furnished with two posterior calcareous "pallets" (Fig. 247, II). Genera—*Teredo*, Linnaeus; a borer in wood; secretes an adventitious non-adherent tube; British. *Xylotrya*, Leach; the pallets articulated.

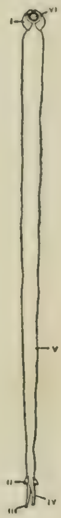

FIG. 247.

Teredo navalis, Linnaeus, ventral aspect. I, shell; II, pallets; III, anal siphon; IV, branchial siphon; V, siphonal mass; VI, foot.

SUB-ORDER 9. ANATINACEA.

Hermaphrodite Eulamellibranchia, in which the ovaries and testes are distinct and have separate orifices (Fig. 219, *o*, *t*). The foot generally rather small. The mantle frequently presents a fourth orifice. The external gill-plate directed dorsally and devoid of a reflected lamella. Hinge of shell without teeth.

FAMILY 1. THRACIIDAE, Dall. Mantle with a fourth pallial orifice; the pedal orifice elongated; siphons rather long, quite separate, and completely retractile and invertible. Shell with a deep pallial sinus. Genera—*Thracia*, de Blainville; shell with a large spoon-shaped tooth; British. *Asthenothaerus*, Carpenter; shell without spoon-shaped teeth. FAMILY 2. PERIPLOMIDAE, Dall. Siphons separate, naked, completely retractile, but not invertible. Pallial sinus shallow; no ligament. Genera—*Cochlodesma*, Couthouy. *Periploma*, Schumacher. *Tyleria*, Adams. FAMILY 3. ANATINIDAE, Gray. Siphons long, united, covered by a chitinous sheath, and not completely retractile. Foot slender. Pallial sinus well marked. Genera—*Anatina*, Lamarck. Shell thin and gaping, with spoon-shaped teeth. *Plectomya*, de Loriol; fossil from the Jurassic and Cretaceous. FAMILY 4. PHOLADOMYIDAE, Gray. Mantle extensively closed, with a fourth orifice. Siphons very long, completely united, naked, and incompletely retractile. Foot small, with a posterior appendage. Shell thin, with an external ligament and a well-marked pallial sinus. Genera—*Pholadomya*, Sowerby; some species living and abyssal; numerous fossil species from the Trias onwards, the maximum in the Jurassic. Family 5. Arcomyidae, Fischer. Shell finely granular, equivalve, thin; the hinge without teeth; the ligament external; pallial sinus. An exclusively fossil family, from the Secondary and Tertiary. Genera—*Arcomya*, Agassiz; from the Trias to the Eocene. *Goniomya*, Agassiz; Jurassic and Cretaceous. Family 6. Pholadellidae, Miller. Shell oval, the posterior extremity attenuated and gaping; cardinal border thin and devoid of teeth; ligament external; posterior adductor muscle large. An exclusively fossil family, from Primary deposits. Genera—*Pholadella*, Hall; Devonian. *Phytimya*, Ulrich; Silurian. *Allorisma*, King; Carboniferous and Permian. Family 7. Pleuromyidae, Zittel. Shell inequilateral, thin; the pallial line deeply sinuous; the cardinal border of one valve covering that of the other and hiding the ligament, which is therefore sub-internal. An exclusively fossil family from Secondary formations. Genera—*Pleuromya*, Agassiz; from the Trias and inferior Cretaceous. *Gresslya*, Agassiz; Jurassic. *Ceromya*, Agassiz; Jurassic. Family 8. Pandoridae, Gray. Shell thin, inequivalve, free; the ligament internal; no pallial sinus. Siphons very short; foot elongate. Genera—*Pandora*, Bruguière; British. *Coelodon*, Carpenter. *Clidiophora*, Carpenter. Family 9. Myochamidae, Dall. Shell very inequivalve, solid, with a pallial sinus. Siphons short; a fourth pallial orifice present; foot small. Genera—*Myochama*, Stutchbury; shell irregular; fixed to other shells by the right valve; Australian. *Myodora*, Gray; shell free, trigonal; the left valve flattened. Family 10. Chamostreidae, Fischer. Mantle largely closed. A fourth pallial orifice present; pedal orifice small. Siphons very short and separate. Shell fixed by the right valve, irregular, without a pallial sinus; ligament internal. Genus—*Chamostrea*, de Roissy; Australian. Family 11. Clavagellidae, d'Orbigny. Mantle largely closed; pedal orifice extremely small; a fourth pallial orifice present; siphons fairly long, united; foot very rudimentary and without a byssus. The ligament external; the valves continued backwards into a calcareous

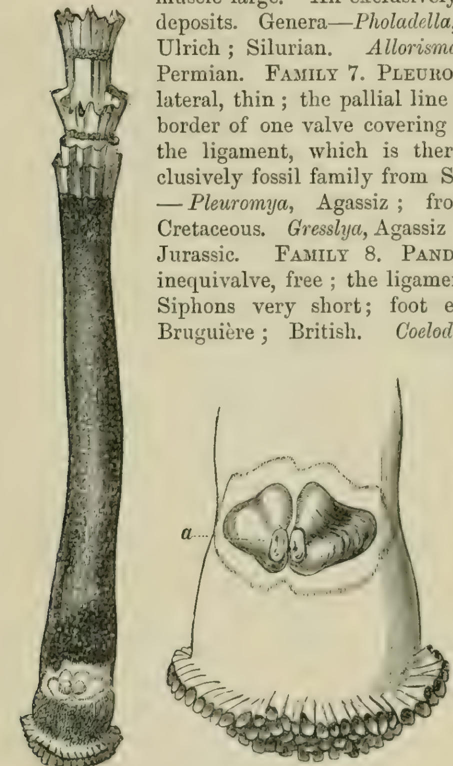

Fig. 248.

Aspergillum vaginiferum; to the left side, the whole shell, dorsal view, the anterior part below; to the right side, the anterior part, magnified, to show the original valves *a*, now embedded in a continuous calcification of tubular form. (From Lankester, after Owen.)

tube secreted by the siphons; pallial line sinuous. Genera—*Clavagella*, Lamarck; left valve fused to the tube; adductor muscles well developed; a boring form. *Brechites*, Guettard (= *Aspergillum*, Lamarck); the two valves fused to the tube and external (Fig. 248); no posterior adductor muscle; the anterior adductor much reduced; the anterior extremity bearing numerous tubular projections serving for adhesion; Indian and Pacific Oceans. FAMILY 12. LYONSIIDAE, Fischer. Mantle largely closed, with a fourth pallial orifice; siphons short, invertible; foot byssiferous. Shell thin, granular externally; the pallial sinus feeble; the ligament internal. Genera—*Lyonsia*, Turton; shell regular and elongated; British (Fig. 219). *Entodesma*, Philippi; shell irregular, truncated behind; a boring form, sometimes found in the tests of Ascidians. *Mytilimeria*, Conrad; shell regular, ventricose, gaping behind. FAMILY 13. VERTICORDIIDAE, Wood. Siphons short; the gills papillose; foot small; palps well developed. Shell globular, very slightly gaping, without a pallial sinus. Many species abyssal. Genera—*Verticordia*, Wood; mantle largely closed; the pedal orifice small. *Euciroa*, Dall; heart situated above the rectum. *Lyonsiella*, Sars; foot byssiferous. *Halicardia*, Dall.

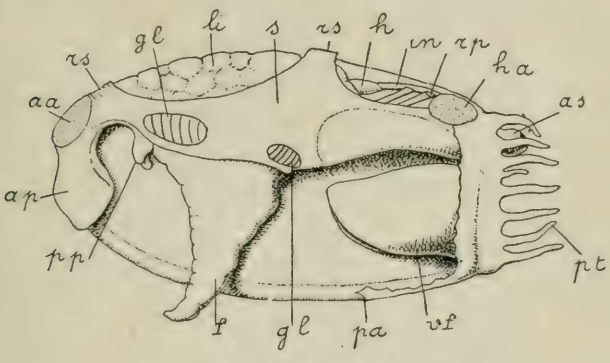

FIG. 249.

Poromya tornata, left-side view. *a.a*, anterior adductor; *a.p*, anterior labial palp; *a.s*, anal siphon; *f*, foot; *g.l*, gill lamellae on the septum; *h*, heart; *ha*, posterior adductor; *in*, intestine; *li*, liver; *pa*, pallial suture; *p.p*, posterior labial palp; *p.t*, pallial tentacles; *r.p*, retractor posterior pedis; *r.s*, retractor of the septum; *s*, septum; *v.f*, valvular fold of the branchial aperture.

ORDER 4. **Septibranchia.**

The Septibranchia are dimyarian Lamellibranchs in which the mantle remains fairly open and has two sutures and two siphons. The foot is long and slender; the byssus rudimentary or absent. The pallial line is simple or very slightly sinuous. The essential character of the group is the disappearance of the gills as respiratory organs, a character which is not found in any other Lamellibranch. The gills are transformed into a muscular septum (Fig. 249, *s*) which extends from the anterior adductor muscle to the point of separation of the two siphons, and surrounds and is continuous with the foot. This septum, therefore, has exactly the situation and the relations of the branchial septum of the majority of the Lamellibranchia, which divides the pallial cavity into two chambers. The group is derivable, more or less directly, from the Anatinacea, through the series *Lyonsia*, *Lyonsiella*, *Poromya*, *Cetoconcha*, *Cuspidaria*, in which one may observe a gradual increase in the amount of muscular fibre in the gill filaments or in their reduced equivalents, so that any objection to the branchial origin of the septum, because of its muscularity, cannot hold good. The muscular septum is inserted on the shell, especially in the neighbourhood of the two adductor muscles. The origin of the anterior and posterior extensions of the septum and of its muscular attachments to the two extremities of the shell is to be found in the physiological contractions necessary to create a current of water on the respiratory surface of the supra-septal chamber. The septum is, in fact, always pierced by paired orifices, which admit of the passage of water. The Septibranchia are all marine, inhabit considerable depths of the sea, and are carnivorous. The order only comprises one sub-order, the Poromyacea.

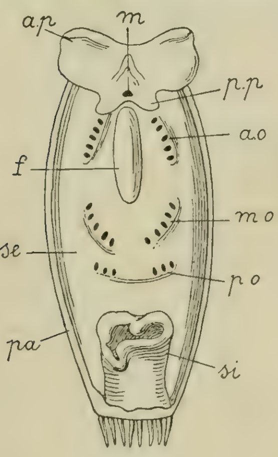

Fig. 250.

A ventral view of *Cetoconcha*, removed from its shell. *a.o*, anterior septal orifices; *a.p*, anterior palp; *f*, foot; *m*, mouth; *m.o*, median septal orifices; *pa*, mantle; *p.o*, posterior septal orifices; *p.p*, posterior palp; *se*, branchial septum; *si*, retractile branchial siphon. (After Ridewood.)

Family 1. Poromyidae, Dall. Siphons short and separate; the branchial siphon provided with a large valve. Foot pointed and not byssiferous. The branchial septum bears two groups of transversely elongate orifices on either side; these are formed by a few branchial filaments, with or without junctions. The palps are large. All the members of the family are hermaphrodite. Genera—*Poromya*, Forbes; no pallial sinus; British (Fig. 249). *Dermatomya*, Dall; a pallial sinus present. *Liopistha*, Meek; fossil from the Cretaceous. Family 2. Cetoconchidae, Ridewood. Branchial septum bearing three groups of orifices on each side; these orifices are separated by rudimentary branchial filaments. Palps large; siphons short, separate, the branchial siphon with a valve. Genus —*Cetoconcha*, Dall (= *Silenia*, Smith); abyssal (Fig. 250). Family 3. Cuspidariidae, Fischer. Siphons long and united, their extremities surrounded by tentacles. Foot narrow, with a rudimentary byssus. Palps greatly reduced or absent. Branchial septum pierced by four or five pairs of very narrow symmetrical orifices. The sexes separate. Genus—*Cuspidaria*, Nardo ; British (Fig. 251).

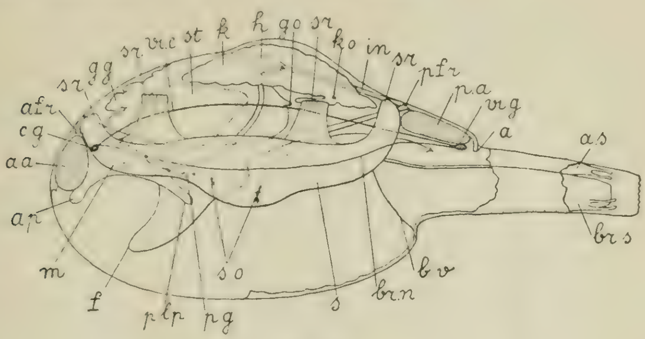

FIG. 251.

Cuspidaria cuspidata (Olivi), left-side view, after removal of left half of the mantle. *a*, anus ; *a.a*, anterior adductor ; *a.f.r*, anterior foot retractor ; *a.p*, anterior labial palp ; *a.s*, anal siphon ; *br.n*, branchial nerve ; *br.s*, branchial siphon ; *b.v*, branchial valve ; *c.g*, cerebral ganglion ; *f*, foot ; *g.g*, genital gland ; *g.o*, genital orifice ; *h*, heart ; *in*, intestine ; *k*, kidney ; *k.o*, kidney opening ; *m*, mouth ; *p.a*, posterior adductor ; *p.f.r*, posterior foot-retractor ; *p.g*, pedal ganglion ; *p.l.p*, posterior labial palps ; *s*, septum ; *s.o*, septal orifice ; *s.r*, septal retractor ; *st*, stomach ; *vi.g*, visceral ganglion.

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CHAPTER VI

THE CEPHALOPODA

CLASS V.—THE CEPHALOPODA, Cuvier.

- Order 1. **Tetrabranchia.**
  - Sub-Order 1. **Nautiloidea.**
  - ,, 2. **Ammonitoidea.**
- Order 2. **Dibranchia.**
  - Sub-Order 1. **Decapoda.**
    - Tribe 1. **Oigopsida.**
    - ,, 2. **Myopsida.**
  - Sub-Order 2. **Octopoda.**
    - Tribe 1. **Leioglossa.**
    - ,, 2. **Trachyglossa.**

Definition.—The Cephalopoda are perfectly symmetrical Mollusca, in which the edges of the foot are transformed into circumoral appendages completely surrounding the head, and the epipodium is modified to form an exhalant muscular tube or funnel consisting of two free or united lobes, situated behind the head at the opening of the pallial cavity, and serving as a conduit for the water from this cavity. In the nervous system all the typical ganglion-pairs are concentrated in the head, and are applied to or contained in the interior of a cartilaginous skeletal piece. The renal organs are constituted by the glandular covering of the afferent branchial vessels. The coelom communicates with the exterior either directly or by the intermediary of the paired kidneys, and by a second pair of ducts serving as gonaducts. The gonad is situated in the coelom and is not continuous with the gonaducts. A portion of the circumoral pedal crown is "hectocotylised," that is to say, modified to form a copulatory organ in the male. The development is characterised by the incomplete segmentation of the ovum.

I. General Description and External Characters.

In comparing the Cephalopoda with other Mollusca, one finds that the ventral surface is much abbreviated and the length of the body reduced (Fig. 22, E). This is the result of the displacement of the foot, whose lateral borders surround the head and are joined together in front of the mouth. In consequence of this shortening of the antero-posterior axis, the two extremities of the digestive canal are closely approximated, and the pallial cavity opens immediately behind the head (Fig. 252, *m*, *a*).

The head is highly developed, but has hardly any other appendages than those formed by the edges of the foot which embrace it. Certain Oigopsida, however, *e.g.* *Taonius suhmii*, Ray Lankester (Fig. 253), and the embryos of an allied form known as Grenacher's embryo (Fig. 119, D) and of *Loligo peali*, have very prominent pedunculated eyes. On the other hand, *Nautilus*, whose eyes are also somewhat prominent, has in addition two ciliated tentacles on either side of the head, one in front of and the other behind the eye (Figs. 255, *i*, *k*; 293, *a.o.t*, *p.o.t*).

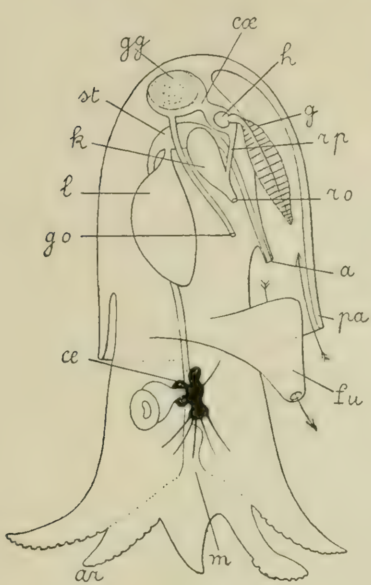


FIG. 252.

Diagram of the structure of a Cephalopod, as seen from the left side in its proper morphological position. *a*, anus; *ar*, arms; *ce*, central nervous system, with eye; *coe*, coelom; *fu*, funnel; *g*, gill; *go*, gonad; *h*, heart; *k*, kidney; *l*, liver; *m*, mouth; *pa*, mantle; *r.o*, renal orifice; *r.p*, renopericardial orifice; *st*, stomach.

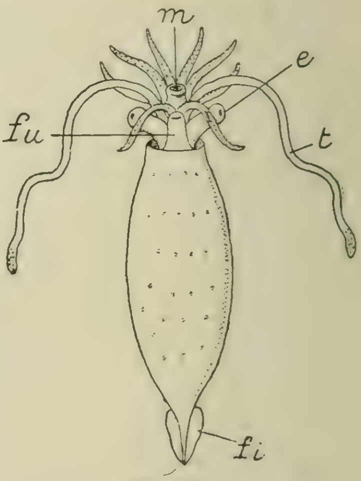


FIG. 253.

Taonius suhmii, Lankester, ventral aspect. *e*, pedunculated eye; *fi*, fin; *m*, mouth; *t*, tentacular arm. (After Hoyle.)

The foot forms a crown of appendages surrounding the mouth: the edges of this crown are not deeply divided in *Nautilus*, but are much more so in the Dibranchia. In *Nautilus* the circumoral pedal crown is divided into lobes each of which bears a group of tentacles, the total number of tentacles being about ninety in the female, but only sixty in the male. These tentacles have laminated but not ciliated surfaces; they are adhesive and prehensile, and are retractile within special tentacular sheaths. When the animal is extended they radiate outwards from the mouth. In the female there are three tentaculiferous lobes in immediate contact with the buccal aperture (Fig. 255, *c*, *d*): these are the right and left and the ventral interior lobes. The last named (which is absent in the male) bears a laminated organ, supposed to be olfactory in function and known as Owen's organ, in the middle of its free border (Fig. 255, *n*), and fourteen tentacles on each moiety of the lobe. The right and left interior lobes bear twelve tentacles apiece. The muscular mass of the foot forms a broad ring round the three interior lobes, and is particularly thick and strong in the dorsal region (Fig. 255, *g*), where it is modified to form a hood which protects the whole animal when it is retracted within its shell. On the external face of the hood is a concavity in which the spire of the shell is lodged. The tentacles borne on this ring are called "digital," and are larger than the "labial" tentacles borne on the three interior lobes. The digital tentacles are nineteen in number on each side in the female, and are disposed more or less regularly in three unequal rows. It is only the dorsal pair of tentacles that belongs to that part of the muscular ring which forms the hood, the last-named

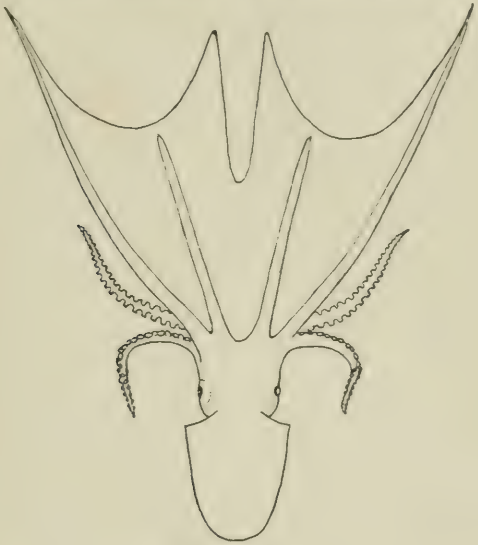


FIG. 254.

Tremoctopus velifer, Verany, viewed from the dorsal side, showing the four dorsal arms joined together by a membrane. (After Verany.)

structure being largely composed of an extension of the sheaths of the tentacles in question. On the ventral side an extensive part of the internal surface of the muscular ring is laminated,

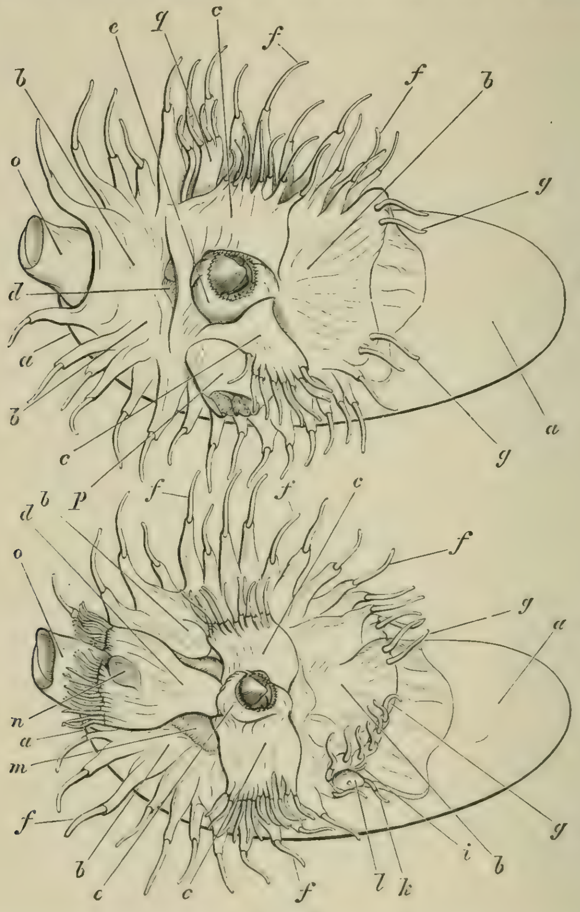


Fig. 255.

Male (upper) and female (lower) specimens of *Nautilus pompilius*, as seen in the expanded condition; oral view, showing the disposition of the tentaculiferous lobes and the differences between the two sexes. *a*, the shell; *b*, the outer ring-like expansion or annular lobe of the circumoral mass of the foot, dorsally forming the hood; *c*, the right and left inner lobes of the foot, each carrying twelve tentacles in the female, in the male divided into *p*, the "spadix" (hectocotylus) on the left side, and *q*, the "anti-spadix," a group of four tentacles, on the right side; *d*, the inner inferior lobe of the foot (reduced in the male to a paired group of lamellae); *e*, the buccal cone, fringing the jaws with a series of minute papillae; *f*, the tentacles of the outer lobe, projecting from their sheaths; *g*, the two most posterior tentacles, belonging to the hood; *i*, superior ophthalmic tentacle; *k*, inferior ophthalmic tentacle; *l*, eye; *m*, paired laminated organ on each side of the base of the inner inferior lobe of the female; *n*, olfactory lamellae upon the inner inferior lobe, in the female; *o*, the funnel; *p*, the spadix (in the male) or hectocotylised portion of the left inner lobe of the foot, representing four modified tentacles; *q*, the antispadix (in the male), being four of the twelve tentacles of the right inner lobe, isolated from the remaining eight. (After Lankester.)

forming the so-called "organ of Valenciennes," peculiar to the female and serving for the attachment of the spermatophores (Fig. 255, *m*).

In the Dibranchia the pedal appendages have the form of four or five pairs of symmetrical and generally elongate arms. In the Octopoda there are eight similar arms, and the whole length of the ventral surface of each is covered by suckers which are often very numerous and highly specialised in structure (Fig. 256). It seems probable that it is the suckers and not the arms that are comparable with the tentacles and tentacle-sheaths of *Nautilus*. In the Decapoda, in addition to the eight arms corresponding to those of the Octopoda, there are two additional "tentacular" arms, of which one is situated between the third and fourth sessile arms on either side of the posterior part of the head. These two tentacular arms are longer and more slender than the others (Fig. 298, A), and the suckers are generally confined to their free extremities, which are enlarged and club-shaped; in some forms, however, they bear suckers along their whole length (Fig. 297, II). The tentacular arms are further distinguished from the sessile arms by the fact that they are more or less retractile within special pouches: they are completely retractile in *Sepia*, *Sepiola*, and *Rossia*, incompletely retractile in *Loligo*, very slightly retractile in the majority of the Oigopsida, and finally they are united to form a beak-like appendage in *Rhynchoteuthis*. In some Oigopsida, such as *Leachia*, *Chaunoteuthis*, some species of *Cheiroteuthis*, and *Grimalditeuthis* (Fig. 258), the tentacular arms are reduced to mere stumps: in the adult *Veranya* they are similarly reduced, but the young still retain small tentacular arms. Similarly a notable reduction of the ordinary or sessile arms, particularly on the dorsal side, may be observed in some Cheiroteuthidae and Cranchiidae. Some or all of the eight sessile arms may be united by a more or less complete interbrachial membrane: the four dorsal arms are united in this manner in *Tremoctopus* (Fig. 254), the six dorsal arms in *Histioteuthis*, and all eight arms in some species of *Eledone*, in *Alloposus*, and in the adult Cirrhoteuthidae and Amphitretidae, the membrane extending in the two last-named families to the tips of the arms, but in the young of *Cirrhoteuthis* (Fig. 260) the membrane is not fully developed.

In the female *Argonauta* the two dorsal arms are enlarged to form a veil (Fig. 301, IV), which is applied to the mantle and secretes a protective calcareous shell. Finally, in most cases a single arm of the male, or a portion of the circumoral pedal crown in *Nautilus*, is modified to form a copulatory organ, which is sometimes detachable. This is the hectocotylus, or spadix in *Nautilus*, which will be described in detail under the head of reproductive apparatus.

The suckers are pedunculated in the Decapoda, the peduncles being axial or lateral, but they are sessile in the Octopoda (Fig. 256). They generally form a double series along the internal, that is to say, the ventral or buccal faces of the arms, but there is a single series in *Eledone* and *Cirrhoteuthis* (Fig. 260). In some cases, however, there are more than two rows, *e.g.* *Spirula* (Fig. 268, *ar*), *Gonatus*, *Dosidicus*, *Tritaxeopus*, *Ctenopteryx* (on the three dorsal pairs of arms), and *Sepia* (Fig. 299, *c*). In point of structure, each sucker consists of a globular or cylindrical projection, comprising an annular surface of application with a central cavity whose capacity can be augmented by the retraction of its floor. The floor is provided with perpendicular muscular fibres (Fig. 256, I), whose contraction causes the sucker to adhere to the prey or to the substratum. The surface of application of the sucker is augmented by the action of radiating muscular fibres (Fig. 256, II), and its adherence is further assured by the cuticular rugosities of this surface. These cuticular structures are simply small projections in the Octopoda, but in the Decapoda there is a complete chitinous ring with denticulated edges which are often very prominent, and in some cases a single denticulation may become very large and preponderant and thus transform the sucker into a hook-bearing organ. In *Onychoteuthis* true functional suckers coexist with the hooks, but in the adult *Veranya* the suckers are nothing more than the bases of the hooks. In various species of *Cheiroteuthis* the tentacular arms bear suckers in which the muscular system is feebly developed and there is neither a central piston nor a horny ring, but the bottom of the cupule is covered by a great number of anastomosed epithelial filaments which constitute an organ for fishing. In *Cirrhoteuthis*, in addition to the row of suckers, there are tentacular filaments on each arm alternating with the suckers.

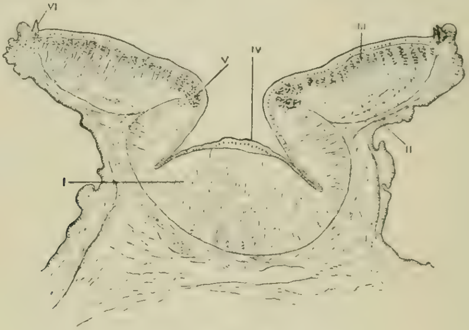


Fig. 256.

Axial section of a sucker of *Argonauta*. I, muscular fibres retracting the bottom of the sucker; II, radiating muscular fibres; III, annular muscular fibres; IV, floor of the cavity of the sucker; V, sphincter muscle; VI, tooth on the margin of the sucker. (After Niemiec.)

In addition to the foot proper, whose edges constitute the circumoral appendages, the Cephalopoda possess an epipodium which is well developed, but highly specialised to form a funnel. The epipodial nature of the funnel may be specially well seen in young embryos (Figs. 257, *fu*; 119, D, *fu*), in which this organ is situated laterally and posteriorly, between the mantle and the foot. Primitively the funnel has the form of two symmetrical lateral lobes, which simply incline towards one another and overlap in *Nautilus* (Fig. 276). In the Dibranchia, however, these two lobes become fused together during development (Fig. 290, (9) *q*) and form a complete tube projecting beyond the pallial cavity (Figs. 253 and 258, etc., *fu*). Through this tube the excrements, the secretion of the ink-sac, and the generative products are ejected. The interior of the funnel is generally provided with a larger or smaller valve, attached to its anterior or dorsal face; as, for instance, in the Nautilidae (Fig. 276, *b*) and the majority of the Decapoda (Fig. 259, *fu*); but this structure is absent in *Leachia* among the Oigopsida and in the Octopoda. In addition, the internal wall of the funnel is furnished with an epithelial outgrowth of variable form, constituting a mucous gland called Müller's organ.

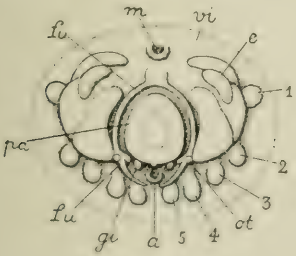


Fig. 257.

Young embryo of *Sepia officinalis*, viewed from the dorsal side. *a*, anus; *e*, eye; *fu*. funnel; *gi*, gill; *m*, mouth; *ot*, otocyst; *pa*, mantle and shell; *vi*, vitellus; 1, 2, 3, 4, 5, arms. (After Kölliker.)

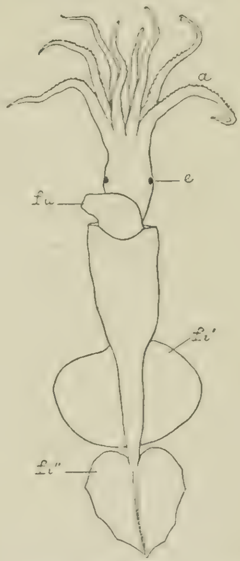


Fig. 258.

Grimalditeuthis richardi, ventral aspect. *a*, arms; *e*, left eye; *fi'*, anterior fin; *fi''*, posterior fin; *fu*, funnel. (After Joubin.)

Powerful muscular bundles, originating from the cephalopedal mass and from the sides of the funnel, unite together and are inserted symmetrically on the sides of the shell (Fig. 272, *m*). In *Nautilus* they are inserted on the interior of the shell, in the Dibranchia on its external surface, in *Spirula* on the margins of the last chamber.

Other differentiated muscular bundles may be recognised; they are mostly due to the specialisation of the funnel.

In the Tetrabranchia (*Nautilus*) the mantle is covered by an external shell, which is partly overlapped by a small dorsal pallial lobe (Fig. 270, *d*): the retractor muscles of the head and foot are inserted symmetrically on either side on the internal surface of this shell. The female *Argonauta* also bears an external shell which covers the mantle, but has no muscular attachments and is not homologous with the shells of other Cephalopods: it does not originate from a pre-conchylian invagination or shell-gland, but is of pedal origin, and is only formed some ten or twelve days after birth by the palmate extremities of the two dorsal arms. The animal is not attached to this shell.

In all other Cephalopoda the shell is covered over by the mantle, or at least is partly covered in *Spirula* (Fig. 295). The shell therefore is internal, and often is rudimentary, as in the majority of Decapoda, or it may be nearly obsolete, as in the Octopoda. The shell of living and fossil Nautiloidea, of Ammonoidea, *Spirula* (Fig. 268, *sp*), and of various fossil Dibranchia, such as the Belemnitidae, *Spirulirostra* (Fig. 262, C), etc., is provided with internal septa, disposed perpendicularly to the axis of the coil. It is only the last of the chambers thus formed that is occupied by the body of the animal, but a prolongation of the pallial integument known as the pallial siphuncle (Fig. 270, *l*) extends back to the initial chamber of the shell, and is enclosed in a calcareous tube or shell siphuncle which perforates all the septa (Fig. 268, *si*). This pallial siphuncle does not communicate with the coelomic cavity: in *Nautilus* and *Spirula* it is a simple vascular vermiform process of the mantle, whose cavity consists of a venous sinus and whose wall contains a ramification of the pallial artery. It apparently plays a part in the hydrostatic function. At the point where the shell siphuncle traverses each septum it is generally surrounded by a small reduplication of the latter, forming the so-called siphuncular neck. The chambers traversed by the siphuncle do not communicate with one another nor with the shell siphuncle: they are filled with a nitrogenous gas and form a hydrostatic apparatus.

The external multilocular shell is straight in some palaeozoic Nautiloidea (*Orthoceras*), but in the majority of Tetrabranchia it is arcuate or more or less completely coiled in such a manner as to form a discoidal shell whose whorls are all in the same plane. In the majority of Tetrabranchia (*Nautilus*, Fig. 270) the coil is exogastric, that is to say, it is turned towards the dorsal aspect, but in some forms, *e.g. Phragmoceras*, *Cyrtoceras*, *Ptenoceras* (Fig. 261, B), it is turned towards the ventral side and is therefore endogastric; the direction of the coil cannot be determined by the position of the siphuncle, which traverses the septa at various points, but by the form of the aperture and the position of the "hyponomous" sinus, which corresponds to the funnel (Fig. 261, *i.s*). In some Nautiloidea, *e.g.* the dextral or sinistral *Trochoceras*, and in sundry Ammonoidea, *e.g.* the sinistral *Turrilites* and *Cochloceras* and the dextral *Bostrychoceras*, the coil may be produced into a helicoidal or turriculated spire. And in other cases again the last whorls of shell, whether it be discoidal or helicoidal, may be partly uncoiled, as may be seen, for example, in *Lituites*, which is largely uncoiled, or in *Ophidioceras*, in which only a small extent of the shell is uncoiled. Finally, the shell may become secondarily rectilinear in the adult, as in *Baculites*, among the Ammonoidea. In *Spirula* the shell is coiled in one plane, but it is endogastric, that is to say, coiled in the opposite direction to that of *Nautilus* (Figs. 268 and 270), and it is largely internal. In certain fossil Dibranchia the multilocular shell, whether it be straight or partially coiled, has become internal (Belemnitidae, *Spirulirostra*) and forms the phragmocone (Fig. 262, C). In such cases it is surrounded by a calcareous secretion of the reflected portion of the mantle, which is not homologous with the shell of other Molluscs, and forms the pointed rostrum or guard at the end opposite to the head (Fig. 262) and the cephalic plate or pro-ostracum at the anterior or dorsal end. Thus there is, in the shells of these Cephalopoda, an element which is not represented in the shells of other Mollusca.

In the living Dibranchia, with the exception of *Spirula*, the phragmocone and the rostrum of this internal shell have become very rudimentary. In *Sepia*, for example, the shell is composed of parallel layers united together by short pillars of calcareous substance, and has a stratified and alveolar structure : at its posterior end a little hollow marks the position of the phragmocone, and a short pointed external projection represents the rostrum, the bulk of the shell being formed by the anterior pro-ostracum, on which the retractor muscles of the cephalopedal mass are inserted. In the Oigopsida the guard is no longer calcified, and the shell has the form of a chitinous plume or gladius, but in *Ommatostrephes* there is a small posterior conical cavity representing the remains of the phragmocone.

In the Loliginidae and Sepiolidae the shell is similarly represented by a chitinous gladius (Fig. 263), but in these families it is so much reduced that it only occupies the anterior portion of the body. In *Idiosepius* this shell is nearly obsolete, and it is absent altogether in certain Sepiolidae and some allied forms such as *Stoloteuthis*, *Inioteuthis*, *Sepioloidea*, and *Sepiadarium*. Finally, in the Octopoda there is no longer a true shell, but only some simple chitinous rudiments, on which the retractor muscles of the head and funnel are inserted ; these may be paired, as in the case of the lateral stylets of *Octopus* ; or unpaired, as in the case of *Cirrhoteuthis*.

It follows that in all living Cephalopods except *Nautilus* the shell is localised on the anterior or physiologically dorsal side of the body, and is enclosed by the mantle, which therefore appears to be a naked, bell-shaped sac (Figs. 252, 254, 287, etc.). The whole circumference of the mantle border is free in the Decapoda (Fig. 259), with the exception of *Sepiola*, in which it is fused to the head anteriorly in the middle line. Similarly, in the Octopoda, the border of the mantle is fused to the head anteriorly and laterally, whereby the pallial aperture is much reduced, especially in *Cirrhoteuthis* (Fig. 260) and *Opisthoteuthis* (Fig. 300).

In the Decapoda a more secure union between the mantle and the funnel, during the expulsion of the water used in respiration through the latter structure, is ensured by the following mechanism: the free borders of the mantle bear on each side a cartilaginous projection (Fig. 272, *c′*) which fits into a corresponding depression in the funnel (Figs. 272, *c*; 259, *so*), the whole constituting the so-called "resisting apparatus" of foreign authors. In certain Oigopsida of the family Cranchiidae (*Cranchia*, *Leachia*) and in the Octopoda this apparatus is but feebly developed, and in *Cirrhoteuthis*, where it would be useless, it has disappeared. Otherwise the funnel is quite independent of the mantle: it is only in *Amphitretus* among the Cirrhoteuthidae that the mantle border is united to the funnel by a ventral suture, leaving an opening into the pallial cavity on either side. Similarly, in *Grimalditeuthis* and *Symplecto-*

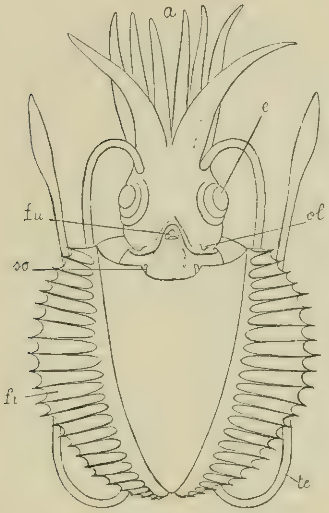


Fig. 259.

Ctenopteryx cyprinoides, ventral aspect. *a*, arms; *e*, eye; *fi*, fins; *fu*, funnel with valve; *ol*, olfactory organ or rhinophore; *so*, socket of the funnel; *te*, tentacular arms. (After Joubin.)

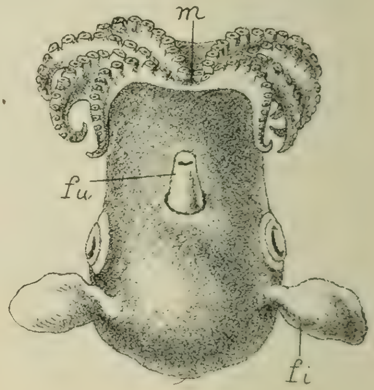


Fig. 260.

Cirrhoteuthis meangensis, Hoyle (young specimen), ventral aspect. *fi*, fin; *fu*, funnel; *m*, mouth. (After Hoyle.)

teuthis among the Oigopsida, there are two infundibulo-pallial sutures.

In the Dibranchia the mantle is a very muscular organ, which, by its contractions, serves two purposes. By alternately and rhythmically drawing in and forcing out the water that enters the pallial cavity between the funnel and the border of the mantle, it acts as an accessory respiratory organ, and by violently expelling water through the funnel it acts as an efficacious locomotory organ, causing the animal to execute sudden retrograde movements.

In the majority of Cephalopods with internal shells (Decapoda) and in the Cirrhoteuthidae, the mantle is produced into lateral symmetrical expansions or fins of various form and position (Figs. 253, 260, and 268, *fi*). These organs always originate at the aboral extremity of the mantle (Fig. 290, (4) *a*)—even in *Octopus*, in which genus they eventually disappear—as two triangular or rounded outgrowths. They remain localised at the aboral extremity in *Spirula*, in which genus they are situated close together at the point where the two halves of the mantle reunite behind the shell (Fig. 295). In most other Oigopsida they are still terminal and close together, but they tend to shift further forward on the anterior or dorsal surface, as in *Taonius* (Fig. 253) and *Ommatostrephes* (Fig. 297), and they may be duplicated, the two fins on each side lying close together, as in *Grimalditeuthis* (Fig. 258, *fi'*, *fi''*) and *Vampyroteuthis*. But in all other cases they diverge to take up positions opposite one another on the right and left sides of the body, and show an increasing tendency to occupy the whole length of the body, as in *Thysanoteuthis*, where they are triangular (Fig. 298, B), and in *Sepioteuthis*, where they are rounded. In *Sepia* the fins extend the whole length of the mantle,

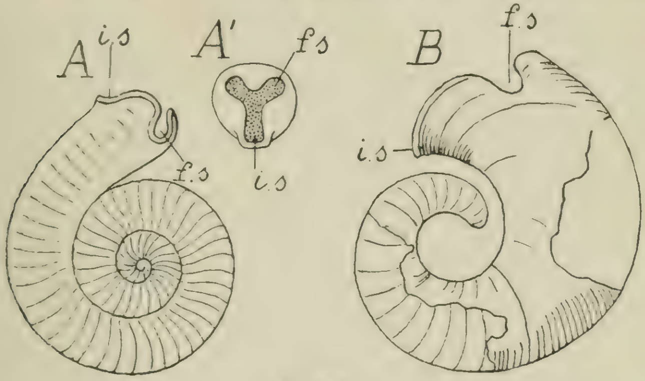


FIG. 261.

Two fossil *Nautilids*, left-side view. *A*, *Ophidioceras simplex*, Barrande ; *A'*, mouth of the shell ; *B*, *Ptenoceras alatum*, Barrande. *f.s*, foot (arms) sinus ; *i.s*, infundibular sinus. (After Barrande.)

but are reduced so as to be of the same width throughout (Fig. 272, P). The fins of *Ctenopteryx* are similar, but are pectinated, that is to say, they consist of a thin membrane supported by muscular fibres (Fig. 259, *fi*). On the other hand, in species with a short and globular mantle the fins are shifted away from the aboral extremity, and are situated either in the middle of the body, as in *Sepiola*, or even near the anterior end, as in *Cirrhoteuthis* (Fig. 260).

Except in *Nautilus* (Fig. 270, *f*) and *Spirula* (Fig. 268, *pa.c*), where it is shallower, the pallial cavity extends from its opening behind the head to the aboral extremity or summit of the body. It contains the branchiae and the anal, renal, and genital orifices (Fig. 272, *Br*, *a*, *r*, *g*). In some forms it is divided longitudinally by a muscular junction between the mantle and the visceral mass, starting from either side of the anus: such is the case in the essentially littoral forms with a short pallial sac, such as *Sepiola* and the Octopodidae. In *Opisthoteuthis* the pallial cavity is particularly narrow and shallow, and the pallial sac scarcely projects; in consequence of the diminution of the ventral flexure the animal is flattened and discoid (Fig. 300), and the anus has returned to the posterior position which it occupies in primitive Mollusca.

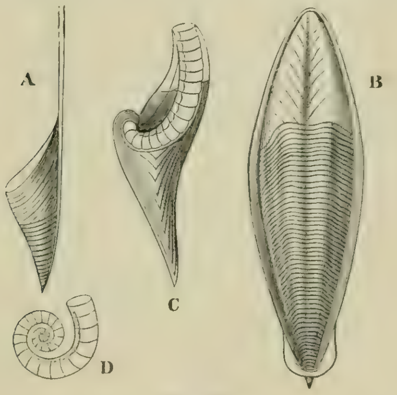


Fig. 262.

Internal shells of Cephalopoda. *A*, shell of *Belemnoteuthis dupiniana* (Neocomian). *B*, shell of *Sepia Orbignyana*. *C*, shell of *Spirulirostra Bellardii* (Miocene); the specimen is cut so as to show in section the chambered shell and the laminated "guard" deposited upon its surface; *D*, shell of *Spirula laevis*. (After Lankester.)

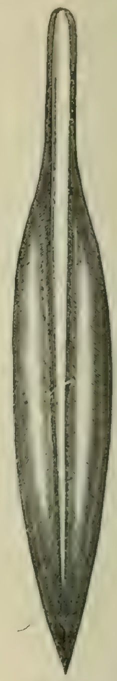


Fig. 263.

The chitinous internal shell, or gladius, of *Loligo*, the anterior part uppermost. (From Lankester, after Owen.)

Beneath the epithelium the integument contains, at least in the Dibranchia, chromatophores or extensible pigment cells, whose activity produces the remarkable colour changes characteristic of these animals. The chromatophores are cells originally of ectodermic origin, which sink below the epithelium and become connected with contractile radiating mesodermic fibres. The pigment cells are simple but multinuclear, since they contain secondary nuclei situated at the bases of the muscular fibres. Different cells contain different coloured pigment: yellow, brown, red, or blue in the Decapoda. Each cell exhibits a constant though feeble tremulous movement, and may suddenly be extended, by a reflex action, under the influence of emotion or excitation, or as a more direct result of volition the chromatophores of the same colour may assume a definite condition of contraction or expansion, which gives the body a tint analogous to that of surrounding objects. In the latter case the action of the chromatophores is under the direct influence of the cerebral centres of the nervous system, and section of one of the optic nerves puts an end to voluntary changes of colour on the same side of the body. The chromatophores are chiefly distributed over the anterior surface (or upper surface when the animal is in its natural position) of the mantle, the head, and the external sides of the arms. In the Decapoda there is, in addition to the chromatophores, a layer of reflecting cells which give these animals their iridescent hues.

In certain Oigopsida belonging to the zonary or deep plankton, for example, *Histioteuthis*, *Calliteuthis*, *Histiopsis*, *Pterygioteuthis*, etc., the surface of the body bears luminous organs, all of which are oriented towards the anterior extremity. The essential structure of these organs consists of a deeper photogenous layer and of superficial refracting elements. They may even extend into the interior of the pallial cavity, as, for example, in *Pterygioteuthis*.

In the deeper parts of the integument the connective tissue is often concentrated to form cartilage of analogous structure to that of the Vertebrates, but characterised by the existence of processes of the cartilage cells which ramify in the matrix and anastomose with one another (Fig. 265). This cartilage is specially well developed in the head. In *Nautilus* there is a capito-pedal cartilage, shaped like a letter H (Fig. 264, A), which only supports the ventral part of the nerve-centres, two of its branches extending into the base of the funnel. In the Dibranchia the cephalic cartilage completely encloses the central nervous system and the otocysts and is traversed by the oesophagus (Fig. 268, *c.c*). In some cases the cephalic cartilage is produced into anterior expansions; such are the pre-orbital cartilages surrounding the eyes of *Sepia* (Fig. 264, C). Various muscles, notably the retractor muscles of the head, take their origin from this "cranial" cartilage. There are also cartilaginous skeletal elements in other parts of the body of various Cephalopoda. In

Loligo, *Sepia*, etc., there are elongated cartilaginous lamellae at the bases of the fins. There is a nuchal cartilage at the base of the neck of all the Dibranchia in which the mantle is not fused to the head; consequently this cartilage is absent in *Sepiola* and the Octopoda (Fig. 264, D). It serves for the insertion of the lateral muscles of the funnel. Cartilaginous pieces also occur at the internal extremities of the retractor muscles of the head and funnel, and even in the two branchial laminae (*Sepia*). In the Decapoda there is sometimes a T-shaped basi-brachial cartilage at the bases of the arms on the anterior (dorsal) side of the head (*Sepia*, Fig. 264, C); it is united to the cranial cartilage and serves for the insertion of the brachial muscles. Finally, the "resisting apparatus" mentioned above is formed by sub-epithelial cartilaginous projections and depressions.

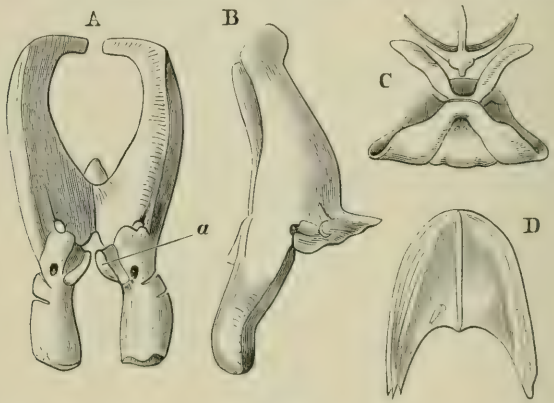


Fig. 264.

Cartilaginous skeleton of Cephalopoda. *A*, capito-pedal cartilage of *Nautilus*, ventral aspect. *a*, ridge which supports the pedal portion of the nerve-centre. *B*, right-side view of the same; the large anterior processes are sunk in the muscular substance of the funnel. *C*, cephalic cartilages of *Sepia officinalis*. *D*, nuchal cartilage of *Sepia officinalis*. (From Lankester, after Keferstein.)

It has been shown that *Lepidoteuthis*, a form not yet sufficiently well known, but apparently a member of the Oigopsida, is exceptional in that the superficial portion of the integument gives rise to a layer of hard, projecting, regularly disposed, imbricated scales, lying above the chromatophores. In *Octopus arborescens* there are ramified and contractile tegumentary papillae.

In several Dibranchia the integument contains certain so-called "aquiferous" cavities, which open to the exterior by special pores, but have no communication with the circulatory system. In addition to the pockets of the tentacular arms of Decapoda, there are cephalic pores on the back of the head and at the base of the funnel in *Ocythoë*, and buccal pouches on the ventral side of the inner base of the crown of arms: one such buccal pouch occurs in *Loligo* and two in *Sepia*, and they may play an accessory part in fecundation. In some exotic species of *Sepia* there are pouches in the mantle.

II. Anatomy.

1. *The Alimentary Canal.*—The digestive tube of Cephalopoda comprises a buccal mass with two mandibles and a radula, a long oesophagus, a muscular stomach with a pyloric caecum, and a short intestine which turns forward and opens in the middle line below the funnel (Fig. 252, *a*).

The buccal aperture, situated in the middle of the pedal appendages (Fig. 260, *m*), is surrounded by a circular lip garnished with papillae. Furthermore, in the decapodous Dibranchia there is a buccal membrane which may be very extensive and be divided into lobes alternating with the arms, and the lobes may even be furnished with small suckers, as may be seen in some species of *Loligo*.

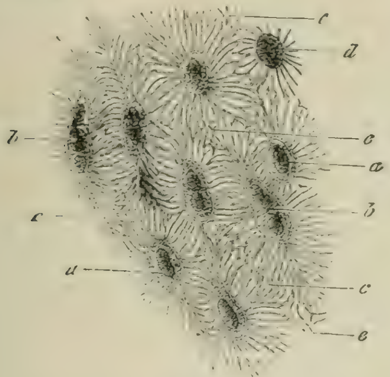


Fig. 265.

Minute structure of the cartilage of *Loligo*. *a*, simple, and *b*, dividing cells; *c*, canaliculi; *d*, an empty cartilage capsule, with its pores; *e*, canaliculi in section. (From Lankester, after Fürbringer.)

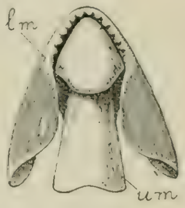


Fig. 266.

Mandibles of *Nautilus*, *in situ*, dorsal aspect. *l.m*, lower or ventral mandible; *u.m*, upper or dorsal mandible. (After Owen.)

The buccal cavity or pharynx has very thick muscular walls. Internally it is provided with two powerful mandibles, one ventral and the other dorsal (Fig. 266): the tip of the ventral mandible overhangs that of the dorsal, forming a beak like that of a parrot (Fig. 268, *vm, dm*). These mandibles have recurved insertion-plates, to which the large muscles forming the greater part of the mass of the buccal bulb are attached. In *Nautilus* the trenchant borders of the mandibles are covered by a calcareous deposit (Fig. 266), and the fossils known by the name of *Rhyncholiths* are nothing else than the beaks of Tetrabranchia: for instance, *Rhyncholithes hirundo* is the beak of *Temnocheilus bidorsatus*, of the Trias.

As in the Amphineura, the Gastropoda, and the Scaphopoda, the floor of the buccal cavity is occupied by the anterior part of the radula, which issues from a pharyngeal caecum. Each transverse series of this radula is formed by a median tooth, with three symmetrically disposed teeth on either side; the only exceptions to this rule being—*Nautilus*, which has four teeth on either side (Fig. 267, A); *Gonatus*, which has only two teeth on either side; the Cirrhoteuthidae, which have no radula and have therefore been named *Leioglossa*. In front of the radular prominence is the so-called "tongue," a fleshy projection (Fig. 268, *to*) covered by a somewhat thick papillated cuticle: it corresponds to the sub-radular organ of other Molluscs.

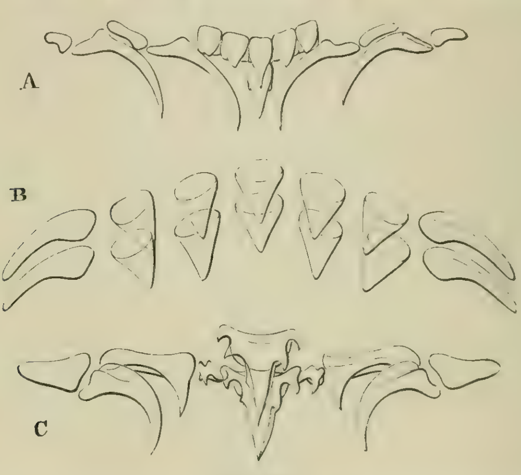


Fig. 267.

Radula of Cephalopoda. *A*, a single row of lingual teeth of *Nautilus pompilius*; *B*, two rows of lingual teeth of *Sepia officinalis*; *C*, lingual teeth of *Eledone cirrhosa*. (From Lankester, after Keferstein, Troschel, and Loven.)

The salivary glands, of which two pairs are present in many Cephalopoda, pour their secretion into the buccal cavity. In *Nautilus* there are no posterior salivary glands, but on each side of the buccal cavity there is the orifice of a gland situated in the buccal wall and corresponding to the anterior salivary glands of the majority of the Dibranchia. In the latter order all the Decapoda have posterior salivary glands, situated fairly far forward opposite the cephalic cartilage (Fig. 268, *s.g*): they are compact, acinous, almond-shaped structures composed of convoluted and bifurcated tubes; their ducts unite immediately they leave the glands to form a single median duct, which runs alongside of the oesophagus and opens, like the duct of one of the pairs of glands in the Aplacophora, at the summit of the sub-radular organ. The anterior pair of salivary glands is relatively slightly developed, and is conspicuous only in the Oigopsida (*Spirula*, Ommatostrephidae, Fig. 282, II, *Onychoteuthis*, *Veranya*, *Gonatus*, etc.). In the Myopsida, however, there is an unpaired intra-bulbar glandular mass, lying behind the radula at the entrance of the oesophagus, and this corresponds to the embryonic condition of the anterior salivary glands of the Oigopsida and Octopoda. The last-named have also two pairs of well-developed salivary glands. The anterior pair consists of two flattened acinous glands attached to the posterior surface of the buccal bulb, their short ducts opening on either side into the postero-lateral part of the pharynx. The topographically posterior or abdominal glands are absent in *Cirrhoteuthis*, but in other Octopoda they are present, and are relatively larger than the similar pair in the Decapoda, but have the same structure and relations, save for the fact that they are situated farther back near the oesophageal proventriculus. The secretion of the posterior salivary glands of the Octopoda contains a proteolytic ferment and is poisonous; the secretion of the corresponding glands of *Sepia* contains, in addition, a diastatic ferment.

In addition to the salivary glands proper, all the Dibranchia possess a sub-lingual gland in front of the sub-radular organ. It is of small size and is formed by the infolding of the epithelium of this region.

The oesophagus is long in all the Cephalopoda, and it may be enlarged to form a crop or proventriculus: this enlargement is gradual in *Nautilus* (Fig. 270, *oe*, *cr*), abrupt in the Octopoda, with the exception of *Cirrhoteuthis*, but in the Decapoda the oesophagus is of the same diameter throughout (Fig. 268, *oe*). The true stomach is a more or less globular or elongated pouch, with fairly thick muscular walls, and is situated at the summit of the visceral mass (Fig. 271, *giz*): its two orifices, the cardiac and the pyloric, are anterior.

At the initial part of the intestine, close to the stomach, is a thin-walled caecal diverticulum of various shape. It is spherical in *Nautilus*, *Rossia*, and *Leachia*, elongated and much larger than the stomach in *Loligo*, but it is more frequently coiled in a spiral, like the spiral caecum of sundry rhipidoglossate and other Gastropoda; such is the case, for example, in *Spirula* (Fig. 268, *p.s*), *Ommatostrephes* (Fig. 269, *c*), *Sepia*, and the Octopoda. The hepatic ducts open into the stomachal caecum.

The liver is formed by two symmetrical glands, which are separate from one another during development (*Sepia*), but are generally partially fused together in the adult. This organ exhibits its minimum state of concentration in *Nautilus*, consisting of four lobes, each with its proper duct. In the Dibranchia the liver is more compact and consists of two lateral lobes, which are only united to a small extent near the middle of their length in

Rossia and *Sepia*, but are much more intimately united in *Sepiola*, and are almost entirely fused together in *Spirula* (in which genus the liver is partly contained in the last chamber of the shell, Fig. 268, *liv*), in *Onychoteuthis*, *Ommatostrephes*, *Loligo*, and the Octopoda, with the exception of *Argonauta*. In these last cases the liver

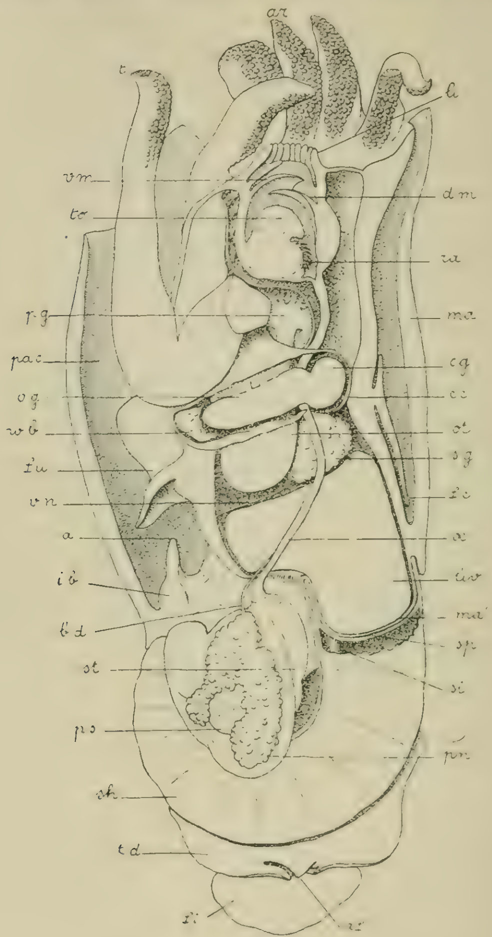


FIG. 268.

Spirula, a nearly median sagittal section, seen from the left side. *a*, anus; *ar*, arms; *a.f*, aboral fossa; *b.d*, bile-duct; *c.c*, cephalic cartilage; *c.g*, cerebral ganglion; *d.m*, dorsal mandible; *f.c*, funnel collar; *fi*, fin; *fu*, funnel; *i.b*, ink-bag; *li*, lip; *liv*, liver; *ma*, mantle; *ma'*, shell secreting part of the mantle; *oc*, oesophagus; *o.g*, optic ganglion; *ot*, otocyst; *pa.c*, pallial cavity; *p.g*, pedal (brachial) ganglion; *pn*, "pancreas"; *p.s*, pyloric sac; *ra*, radula; *s.g*, salivary gland; *sh*, shell; *si*, shell siphuncle; *sp*, last septum of the shell; *st*, stomach; *t*, tentacular arm; *t.d*, pallial terminal disc; *to*, tongue; *v.m*, ventral mandible; *v.n*, visceral nerve; *w.b*, white body. (After Huxley and Pelseneer.)

appears to be an undivided ovoid or globular mass, but it is traversed by the oesophagus, and its double origin is further demonstrated by the hepatic ducts, which are two in number, in all the Dibranchia. In the Decapoda the hepatic ducts are long (Fig. 268, *b.d*) and traverse the kidneys; in the Octopoda they are short. In the former sub-order the ducts are covered by the so-called "pancreatic" glandular follicles, whose structure is a little different from that of the liver (Fig. 268, *pn*). In the Octopoda these follicles are situated only on the initial part of the hepatic ducts and are nearly buried in the mass of the true liver. Digestion is wholly effected in the muscular stomach by the action of the trypsin secreted by the liver and by the diastatic ferment secreted both by the liver and the "pancreatic" follicles.

The intestine is relatively short and of uniform diameter. In *Nautilus* and the Octopoda it is slightly sinuous, but in the Decapoda it is straight. The anus is situated in the middle line towards the anterior part of the pallial cavity (Fig. 272, *a*), and is often furnished with lateral valves. With the exception of *Nautilus*, *Cirrhoteuthis*, *Octopus arcticus*, and *O. piscatorum*, all the Cephalopoda, including the fossil Belemnites, have an ink-sac, consisting of a highly-developed rectal caecum developed early in embryonic life from the dorsal wall of the intestine and opening into the extreme terminal part of the rectum. This sac is made up of a deeper part, or gland proper, the cavity of which is septate, and a reservoir, into which the glandular part opens by a very small orifice: the reservoir specially well developed in the Decapoda. This ink-sac occupies a somewhat superficial position to the side of the visceral mass. In some species of *Sepiola* it is trilobed, two lateral accessory organs being joined to it. It extends to the posterior extremity of the body in *Sepia* (Figs. 271, *i.s*; 272, *t*), and is buried in the superficial part of the liver in all the Octopoda except *Argonauta*. The Cephalopoda are able, at will, to expel the secretion contained in the reservoir of this anal gland through the funnel, and thus conceal themselves by producing a dense cloud in the water. An oxydising diastase, called tyrosinase, is concerned in the production of the secretion, the latter being known as melanin.

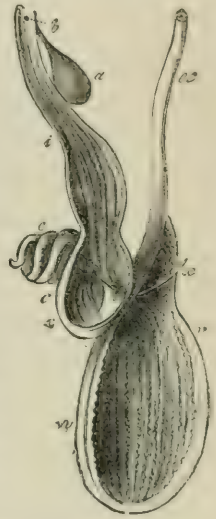


FIG. 269.

Alimentary canal of *Ommatostrephes sagittatus*; the buccal mass is omitted. *a*, ink-bag; *b*, its opening into the rectum; *c*, commencement of the caecum; *e*, spiral portion of the caecum; *oe*, oesophagus; *v*, the stomach opened longitudinally; *x*, probe passed through the pylorus. (From Lankester, after Home.)

2. *Circulatory Apparatus.*—The Cephalopoda, or at any rate the

Dibranchia, have a more complete and perfect circulatory system than other Mollusca, the blood being nearly entirely contained in true vessels.

The heart is situated somewhat superficially near the middle of the posterior or physiologically ventral surface (Fig. 252, *h*). It lies in a pericardial cavity (Fig. 252, *coe*), except in the Octopoda, in which sub-order this cavity is much reduced (Fig. 278, *ca*). The essential part of the heart is the median ventricle (Fig. 277, *ven*), the lateral and symmetrical auricles being nothing more than simple

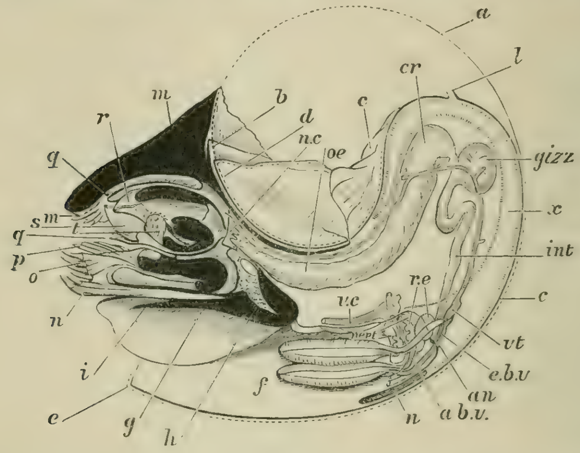


FIG. 270.

Diagram representing an approximately median sagittal section of a female *Nautilus pompilius*. The parts which are quite black are the cut muscular surfaces of the foot and buccal mass. *a*, the shell; *an*, anus; *a.b.v*, afferent branchial vessel; *b*, the nuchal plate; *c*, the integument covering the visceral hump; *cr*, crop; *d*, the mantle flap or skirt in the dorsal region, where it rests against the coil of the shell; *e*, the inferior margin of the mantle-skirt resting on the lip of the shell represented by the dotted line; *e.b.v*, efferent branchial vessel; *f*, the pallial chamber with two of the four gills; *g*, the vertically cut median portion of the funnel; *gizz*, gizzard; *h*, the capito-pedal cartilage; *i*, the valve of the funnel; *int*, intestine; *l*, the siphuncular pedicle (cut short); *m*, the hood or dorsal enlargement of the outer lobe of the foot; *n*, tentacles of the outer lobe; *n.c*, nerve-collar; *nept*, aperture of the kidney; *ni*, nidamental gland; *oe*, oesophagus; *p*, tentacles of the inner inferior lobe; *q*, buccal membrane; *r*, upper jaw; *r.e*, renal glandular masses on the walls of the afferent branchial veins; *s*, lower jaw; *t*, radula; *vt*, ventricle of the heart; *x*, the viscero-pericardial sac. (After Lankester.)

contractile expansions of the efferent branchial vessels (Fig. 277, *au*). In *Nautilus* there are four such auricles, returning blood from the four branchiae, but in the Dibranchia there are only two. In general the ventricle is slightly asymmetrical, except in *Nautilus* (Fig. 274, *vent*), in which it is transversely elongated, and in *Loligo*, in which it is elongated antero-posteriorly. The entrances of the auricles into the ventricle and origins of the aortae from it are guarded by valves. The aortic vessels consist of—(1) a cephalic or principal aorta, which runs forward (Fig. 277, *a.a*) and supplies the whole of the anterior part of the body with blood; (2) a posterior or abdominal aorta, which is smaller, especially in the Octopoda, and carries blood to the posterior part of the mantle, including the siphonal prolongation of *Nautilus* and *Spirula* and the fins of the various Dibranchia; (3) a small genital artery, which may originate from the abdominal aorta (Fig. 277, *g.a*), or separately from the ventricle: it may even be triple, as in *Nautilus*, where there is one artery for the gonad, one for its duct, and one for the homologue of the duct, the pyriform appendage.

In *Nautilus* the circulation is partly lacunar, except in the integuments, but in the Dibranchia the vascular apparatus is remarkably perfect, and sinuses are, as a rule, absent, the blood passing from the arteries into the veins through the intermediary of capillary vessels provided with an endothelium. Nevertheless, in the Octopoda there is a large venous sinus on the course of the blood returning to the gills: this sinus surrounds the oesophagus and salivary glands, the hepatic ducts, the anterior aorta, etc., and communicates by a large venous trunk with the great vena cava which carries to the gills the greater part of the blood coming from the body. In *Nautilus* the whole visceral cavity is a vast blood-sinus communicating with the vena cava by a number of perforations in the walls of the latter vessel, in the same manner as, in *Aplysia*, the abdominal sinus communicates with the afferent branchial vein. The vena cava of Cephalopods consists of a principal trunk directed antero-posteriorly: this trunk in *Nautilus* (Fig. 274, *v.c*) is divided into four, and in the Dibranchia into two afferent branchial veins, each of which is joined by a pallial and an abdominal vein (Fig.

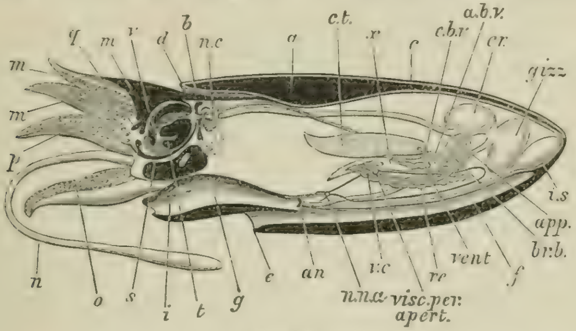


FIG. 271.

Diagram representing an approximately median sagittal section of *Sepia officinalis*; this drawing is intended to be compared with the foregoing one. *a*, internal shell; *a.b.v*, afferent branchial vessel; *an*, anus; *app*, appendage of the branchial heart; *b*, nuchal cartilage; *br.b*, branchial heart; *c*, the integument covering the visceral hump; *cr*, crop; *ct*, the left ctenidium; *d*, the reflected portion of the mantle-skirt forming the sac which encloses the shell; *e*, the inferior margin of the mantle-skirt; *e.b.v*, efferent branchial vessel; *f*, the pallial chamber; *g*, the vertically cut median portion of the funnel; *gizz*, the gizzard; *i*, the valve of the funnel; *i.s*, ink-bag; *m*, the two upper lobes (arms) of the foot; *n*, the long prehensile arms; *n.c*, the nerve-collar; *n.n.a*, aperture of the left kidney; *o*, the fifth or lowermost lobe (arm) of the foot; *p*, the third arm; *q*, buccal membrane; *re*, renal glandular mass; *s*, the lower jaw; *t*, the radula; *v*, the upper jaw; *vent*, ventricle of the heart; *visc.per.apert*, viscero-pericardial aperture; *x*, the viscero-pericardial sac. (After Lankester.)

277, *v.c*, *p.v*, *ab.v*). Each afferent branchial vessel and the terminal portion of each abdominal vein is enclosed in the cavity of a kidney and is covered externally by an excretory glandular coat (Figs. 273, *a.r*; 277, *s.b*) which forms the "spongy body" or essential part of kidney (see below). Except in *Nautilus*, each afferent vessel is

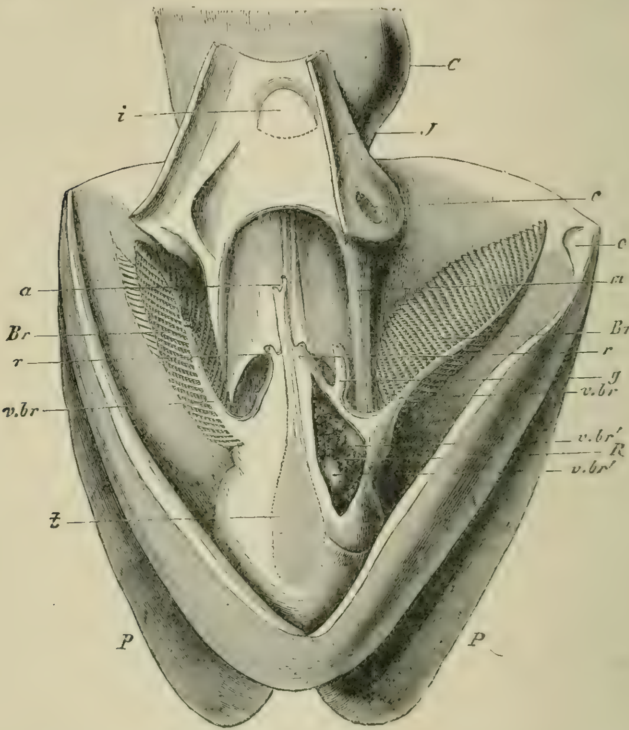


FIG. 272.

Ventral view of a male *Sepia*, obtained by cutting longitudinally the firm mantle-skirt, and drawing the divided halves apart. *a*, anus; *Br*, the single pair of ctenidia; *c*, cartilaginous socket in the funnel, to receive *c′*, the cartilaginous knob of the mantle-skirt,—the two constituting the "pallial hinge apparatus"; *C*, the head; *g*, the azygos genital papilla and aperture; *i*, the valve of the funnel; *J*, the funnel, which has been cut open; *m*, retractor muscle of the head and funnel; *P*, the fins; *r*, renal papillae; *R*, the glandular tissue of the left kidney, which has been cut open; *t*, ink-bag; *v.br*, branchial efferent vessel; *v.br′*, bulbous enlargements (auricles) of the branchial vessels. (From Lankester, after Gegenbaur.)

expanded at the base of the gill into a contractile glandular swelling known as the "branchial heart," which is also provided with a glandular appendage, the homologue of the pericardial gland of other Mollusca (Fig. 277, *b.h*, *a.p*). Both branchial heart and appendage are contained in the coelom (Fig. 273, *c.r*) in the Decapoda, but in the Octopoda only the appendage of the branchial heart is surrounded by the pericardial cavity (Fig. 278, *ca*). In addition to the branchial hearts, a large part of the venous system is contractile, and this is notably the case with the vena cava and its two afferent branches.

The venous blood is blue through the presence of haemocyanin, which becomes colourless on oxidation (oxyhaemocyanin). The pressure of the blood in the arteries of the Cephalopoda is very considerable and exceeds that of some Vertebrates: in *Octopus* it amounts to eight centimetres of mercury. In the head of the Dibranchia there is a lymphatic gland near each eye: this gland is known as the "white body" (Fig. 268, *w.b*) and is the remains of a degenerate portion of the central nervous system of the embryo.

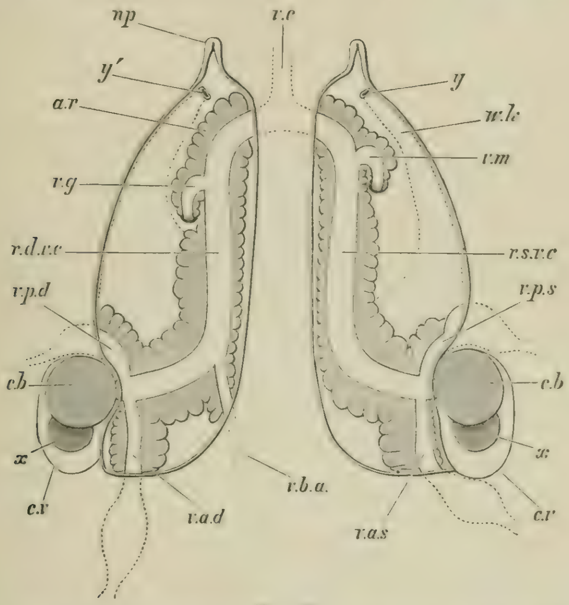


FIG. 273.

Diagram of the renal sacs, and the veins which run through them, in *Sepia officinalis*; ventral view, the upper walls of these sacs are supposed to have been removed. *a.r*, glandular renal outgrowths; *c.b*, branchial heart; *c.v*, capsule of the branchial heart; *np*, external aperture of the right renal sac; *r.d.v.c*, right descending branch of the vena cava; *r.s.v.c*, left descending branch of the vena cava; *v.a.d*, right abdominal vein; *v.a.s*, left abdominal vein; *v.b.a*, vein from the ink-bag; *v.c*, vena cava; *v.g*, genital vein; *v.m*, mesenteric vein; *v.p.d*, right pallial vein; *v.p.s*, left pallial vein; *w.k*, viscero-pericardial sac (dotted outline); *x*, appendage of the branchial heart; *y*, *y′*, the left and right reno-pericardial orifices. (From Lankester, after Vigelius.)

The branchiae or ctenidia are situated in the pallial cavity on either side of the visceral mass. They originate posteriorly in the embryo, between the mantle and the foot (Fig. 257, *gi*), and afterwards sink in towards the bottom of the pallial cavity where their axes are inserted (Figs. 272, *Br*; 276), their free ends pointing towards the head. *Nautilus*, the only living representative of the

Tetrabranchia, has two pairs of branchiae (Fig. 276). All other Cephalopods have a single pair of branchiae, and thus constitute the order Dibranchia, much richer in living species than the Tetrabranchia. The branchiae are bipectinate (Fig. 272, *Br*), but in some Dibranchia the two sides of the organ are somewhat unequal in size. A branchia is composed of lamellae whose number varies in different forms, being least in the Octopoda, in which the axial branchial cavity, separating the two rows of lamellae, is excessively developed. Each branchial lamella is thrown into transverse folds, which are in turn folded, so that the respiratory surface is largely increased.

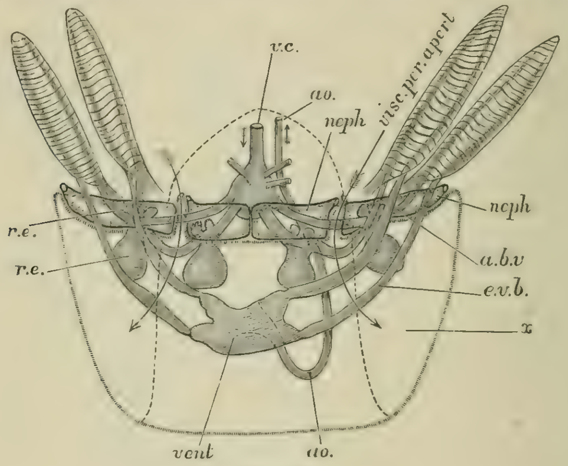


FIG. 274.

Diagram showing the relations of the four nephridial sacs, the viscero-pericardial sac, and the heart and large vessels in *Nautilus*; ventral view. *a.b.v*, advehent branchial vessel; *a.o*, cephalic aorta; *e.v.b*, efferent branchial vessel; *neph*, the two left renal sacs, each with its independent aperture; *r.e*, glandular enlarged walls of the advehent branchial vessels (two small bodies in each renal sac; and one large body on each of the four vessels, in the viscero-pericardial sac); *v.c*, vena cava; *vent*, ventricle of the heart; *visc.per.apert*, arrow introduced in the left aperture of the viscero-pericardial sac; *x*, viscero-pericardial sac (the dotted line indicates its backward extension, *vide* Fig. 270, *x*). (After Lankester.)

The branchiae are not ciliated, as they are in other Mollusca, the contractions of the muscular mantle sufficing to produce a current of water sufficient for respiration. The rate of the respiratory movements of the mantle is variable, and is generally quicker in the Decapoda than in the Octopoda.

In *Nautilus* (Fig. 276) the branchiae are free throughout their extent, but in the Dibranchia they are attached dorsally to the mantle by their afferent borders (Fig. 272). A special glandular organ, whose function is not exactly known, is situated along the line of attachment: it receives the blood which, having circulated through the nutrient vessels of the gill, has to pass through the kidney along with the venous blood from the mantle, to be returned thence into the respiratory vessels of the branchia for oxygenation before it is finally carried to the heart.

3. *Excretory Apparatus.*—The coelom of the Cephalopoda is very extensive. It comprises the gonocoele and the pericardial coelom; these cavities communicate freely with one another (Fig. 252, *coe*) and are only separated by an incomplete septum, which is atrophied in *Sepia*. In *Nautilus* this coelom extends into the aboral region of the body and its genital division—which communicates with the pericardial division by three orifices in the septum—passes into the dorsal region and extends nearly as far forward as the middle of the oesophagus (Fig. 270, *x*). But the pericardial coelom is a flattened ventral cavity situated immediately beneath the body-wall: it contains the heart with its four auricles (Fig. 274) and the pericardial glands or portions of the follicular glandular appendages of the branchial vessels. In the Dibranchia, the coelom of the Decapoda contains the heart, the gonad, and the branchial hearts with their glandular appendages (pericardial glands, Fig. 273, *c.b*, *x*), but it is so much reduced in the Octopoda that it contains only the gonads and the appendages of the branchial hearts, its anterior part having disappeared (Fig. 278).

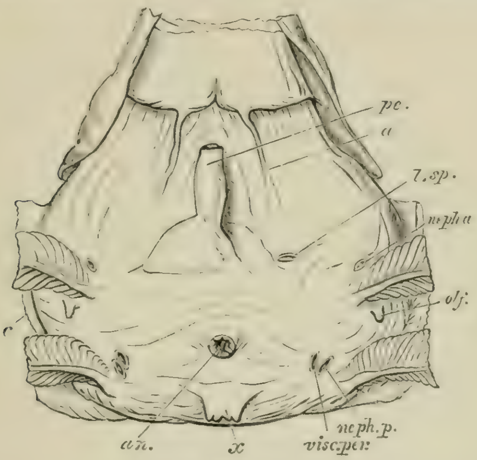


FIG. 275.

View of the ventral surface of a male *Nautilus*, the mantle-skirt being completely reflected so as to show the inner wall of the sub-pallial chamber and the four ctenidia and the foot cut short. *a*, muscular band, passing from the funnel to the integument; *an*, anus; *c*, mantle-skirt; *l.sp*, aperture of the rudimentary left spermiduct; *neph.a*, aperture of the left anterior kidney; *neph.p*, aperture of the right posterior kidney; *olf*, protective papilla of the osphradium; *pe*, penis; *visc.per*, left aperture of the viscero-pericardial sac; *x*, post-anal papilla. (After Lankester.)

In the Decapoda the coelom forms a vast pouch, with a constriction between the posterior or genital division and the anterior pericardial division, and it is produced into lateral annexes for the lodgment of the branchial hearts (Fig. 273, *c.v*). In the Octopoda the anterior division no longer exists; the genital capsule is connected with the capsules of the appendages of the branchial hearts by long canals (Fig. 278, *a.d*), and even these are suppressed in *Philonexis* and *Argonauta*.

In all Cephalopods each of the two divisions of the coelom is in open communication with the exterior. In the Dibranchia this communication is effected through the kidneys: there is a reno-pericardial canal on either side which opens into the cavity of the kidney, more or less close to its external orifice (Figs. 273, *y*; 277, *r.p*). But in *Nautilus* the pericardium opens directly to the exterior by means of two symmetrical orifices situated close to the posterior renal apertures (Fig. 276, *visc.per*); these must be regarded as the orifices of the reno-pericardial ducts which have migrated to the surface. In the Octopoda, in which the pericardial division of the coelom

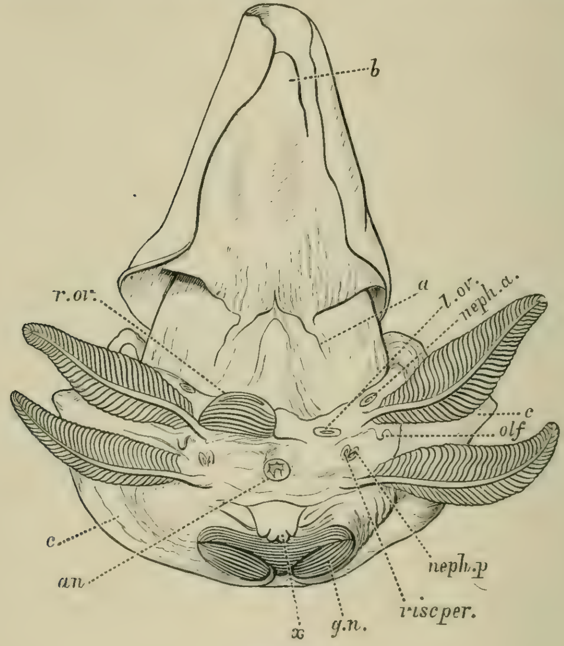


Fig. 276.

View of the ventral surface of a female *Nautilus*, the mantle-skirt being completely reflected so as to show the inner wall of the sub-pallial chamber (compare with *Sepia*, Fig. 272). *a*, muscular band passing from the funnel to the integument; *an*, anus; *b*, valve of the funnel; *c*, the mantle-skirt retroverted; *g.n*, nidamental gland; *l.ov*, aperture of the rudimentary left oviduct; *neph.a*, aperture of the left anterior kidney; *neph.p*, aperture of the left posterior kidney; *olf*, protective papilla of the left osphradium; *r.ov*, aperture of the right oviduct; *visc.per*, left aperture of the viscero-pericardial sac; *x*, post-anal papilla. (After Lankester.)

has disappeared, the anterior extremities of the capsules of the branchial hearts communicate with the kidneys (Fig. 278, *r.p*).

The renal capsules are thin-walled and somewhat voluminous sacs in all the Cephalopoda. In *Nautilus* they are four in number, are ventral and superficial, and have no communication with one another or, as has been explained, with the pericardium. Each of the four capsules has its own simple slit-like orifice (Figs. 275 and 276, *neph.a*, *neph.p*), and each contains a small portion of the glandular appendages of the afferent branchial vessels, the appendages being formed by ramifications of these same vessels, covered by an excretory renal epithelium. The appendages situated on the other side of these vessels, in the pericardial coelom, are also excretory organs, and constitute the pericardial glands.

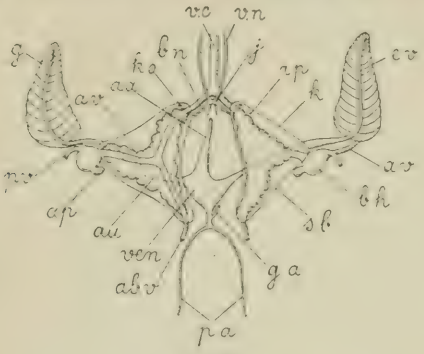


FIG. 277.

Heart, kidneys, and gills of *Spirula*, ventral aspect. *a.a*, anterior aorta ; *ab.v*, abdominal vein ; *a.p*, branchial heart-appendage ; *a.v*, afferent branchial vessel ; *au*, heart-auricle ; *b.h*, branchial heart ; *b.n*, branchial nerve ; *e.v*, efferent branchial vessel ; *g*, gill ; *g.a*, genital artery ; *j*, junction of the visceral nerves ; *k*, kidneys ; *k.o*, kidneys opening ; *p.a*, pallial arteries ; *p.v*, pallial vein ; *r.p*, reno-pericardial opening ; *s.b*, spongy renal glandular bodies ; *v.c*, vena cava ; *ven*, heart-ventricle ; *v.n*, visceral nerve. (After Huxley and Pelseneer.)

In the Dibranchia there are two renal capsules, also ventral and superficial ; these two kidneys are attached to one another in the median line in the Octopoda, and they communicate to a greater or less extent with one another in the Decapoda, with the exception of *Spirula* (Fig. 277, *k*). In the majority of the Decapoda the renal sacs extend as far as the lower surface of the shell, on the anterior or physiologically dorsal side, and are traversed in this region by the hepatic ducts. Each contains one of the two divisions of the vena cava (Fig. 273, *r.s.v.c*, *r.d.v.c*) as well as the terminal part of the abdominal vein. All these vascular trunks are covered by spongy glandular appendages (Fig. 273, *a.r*), whose structure is similar to that of the corresponding parts of the renal organs of *Nautilus*; these appendages constitute the secretory portion of the kidneys. The external orifices of the renal sacs of the Dibranchia are situated at their cephalic extremities; they are symmetrically disposed on either side of the rectum (Fig. 272, *r*), on the somatic wall of the pallial cavity, and are more or less close to the pallial aperture, being further from the aperture in *Ommatostrephes* (Oigopsida) than in *Sepia* (Myopsida). In the Decapoda Myopsida the renal orifices are situated on prominent papillae.

The excretory products of the Cephalopoda consist, in part at least, of solid concretions, and do not contain uric acid, but chiefly guanin.

The appendages of the branchial hearts of the Dibranchia (Fig. 273, *x*) correspond morphologically with the pericardial glands of other Mollusca. The glandular investment of the branchial hearts is also excretory, experiment having shown that it plays the same physiological part as a pericardial gland.

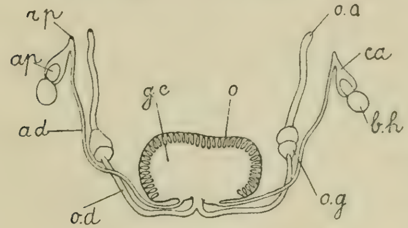


FIG. 278.

Diagram of the coelom of a female Octopod, as seen from the ventral side. *a.d*, the so-called aquiferous duct; *a.p*, appendage of the branchial heart; *b.h*, branchial heart; *ca*, capsule of branchial heart; *g.c*, genital coelom (gonocoele); *o*, ovary; *o.d*, oviduct; *o.g*, oviducal gland; *o.o*, oviducal orifice; *r.p*, renopericardial orifice. (After Brock.)

4. *Nervous System.*—In all the Cephalopoda the essential parts of the nervous system are centralised in the head, round the initial part of the oesophagus (Fig. 271, *n.c*). In *Nautilus* the concentration of the nerve-centres is less than in the Dibranchia, each pair of centres with its commissure being represented by a ganglionic half-hoop. Of the three half-hoops forming the central nervous system, one, the cerebral, is dorsal, and the two others are continuous with it and ventral. The more anterior ventral half-hoop is the pedal centre, the more posterior the visceral. The pedal centre innervates the funnel and the circumoral appendages, the pedal origin of these organs being demonstrated by this innervation in the adult. In the female each of the two large nerves passing to the interior ventral series of tentacles bears a large ganglion at the point where it breaks up into branches to supply the supposed olfactory or lamellar organ (Fig. 280, *x*, *y*). The visceral centre gives off nerves to the mantle, the branchiae, and the viscera, the distribution of these nerves being analogous to that of the Dibranchia described below. Finally, the dorsal or cerebral centre gives off nerves to the eyes, the otocysts, the lips, etc. A labial commissure is also present, arising by a double root (Fig. 279, VIII) from the cerebral centre and passing below the sub-radular organ; and as is the case in the Polyplacophora, the Aspidobranchia, and the Scaphopoda, the stomato-gastric commissure arises from the labial commissure in

all Cephalopods. In *Nautilus* the stomato-gastric commissure passes under the pharynx immediately behind the radula and bears a buccal ganglion (Fig. 279, VII) on either side.

In the Dibranchia the nerve-centres are much more completely enclosed in the cartilaginous cephalic capsule than in *Nautilus*, and consequently many nerves—notably the pallial nerve—traverse the cephalic cartilage at their origin. The cerebral centres themselves appear externally to be unpaired, and in the Decapoda they are divided transversely into a small anterior (Fig. 282, III) and a large posterior lobe, the latter being separated by some considerable distance from the former in various Oigopsida, such as *Ommatostrephes* (Fig. 282, IV), *Spirula*, etc., but the distance is less in *Sepiola* and *Loligo*, and is very small in *Sepia*. These two lobes are united by a pair of slender connectives, which are sometimes fused together for a certain distance. In the Octopoda, on the other hand, the cerebral mass is apparently single, the two lobes above mentioned being intimately fused together, and their limits are barely indicated by a transverse furrow, behind which is the posterior lobe with six longitudinal furrows on its surface. The cerebral centres of all the Dibranchia give off a large optic nerve on either side, each nerve expanding to form a very large ganglion, whose size is greater than that of the whole mass of the cerebral centres. As in *Nautilus*, a labial commissure is given off from the anterior part of the cerebral centres (Fig. 279, IX), and the stomato-gastric commissure originates from the labial commissure. Finally, the cerebro-pedal pair of connectives issues from the anterior part of the cerebral mass; these connectives are simple in the Octopoda (Fig. 281), but in the

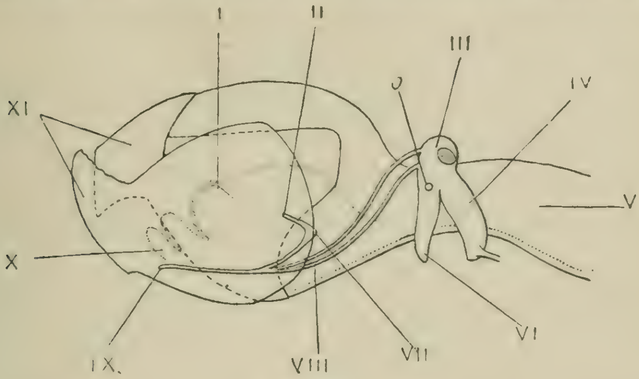


FIG. 279.

Nautilus, central nervous system, left-side view. I, radula; II, stomato-gastric commissure; III, cerebral ganglion, with the optic nerve in section; IV, visceral ganglion; V, oesophagus; VI, pedal ganglion; VII, stomato-gastric ganglion; VIII, root of the labial commissure; IX, labial commissure; X, "tongue"; *o*, otocyst.

Decapoda there are two on each side, namely, the cerebro-pedal and the cerebro-brachial. The ventral or sub-oesophageal nervous mass is formed by the visceral and pedal centres: these are fairly closely united together (as they are, for instance, in *Helix*), and are only separated in the middle line to admit of the passage of an aortic vessel which runs dorsad of the visceral and ventrad of the pedal centres; a similar arrangement occurs in sundry Gastropods.

The pedal ganglia are divided transversely into two distinct pairs, the anterior or brachial and the posterior or pedal ganglia proper (Fig. 282, XII, XIV). This division is most marked in the Oigopsida (*Ommatostrephes*, *Spirula*, Fig. 268, *p.g*, etc.), but is less marked in *Sepia*. In all the Decapoda the brachial centres are divided anteriorly into ten large nerves which pass into the arms, and anastomose with one another at their bases. These centres also have connectives joining them to the anterior and the posterior cerebral lobes (Fig. 282). In the Octopoda the brachial and pedal centres are much more closely approximated (Fig. 281), and the former naturally give off only eight nerves to the eight arms. The brachial nerve-centres extend, together with the arms which they innervate, round either side of the oesophagus, and in the Octopoda they meet dorsally and

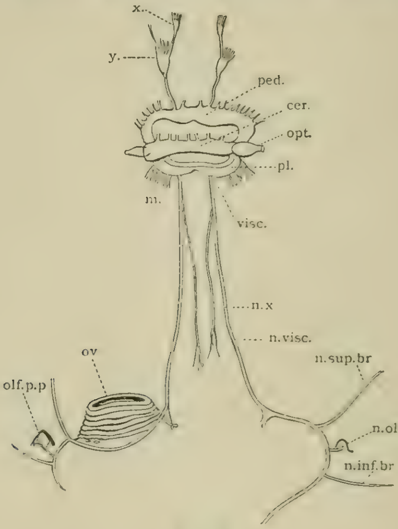


Fig. 280.

Diagram of the nervous system of a female *Nautilus pompilius*, ventral aspect. *cer*, cerebral ganglion; *m*, nerves to the mantle; *n.inf.br*, posterior branchial nerve; *n.olf*, olfactory nerve terminating under the olfactory papilla; *n.sup.br*, anterior branchial nerve; *n.visc*, genito-branchial nerve, or chief visceral nerve; *n.x*, nerve accompanying the vena cava, which lies between this and the similar nerve of the right side; *olf.p.p*, the right olfactory papilla; *opt*, optic ganglion; *ov*, the oviduct; *ped*, pedal ganglion; *pl*, pallial part of the visceral ganglionic commissure; *x* and *y*, ganglion-like enlargements on pedal nerves to the median lobe of the inner circlet of the circumoral tentacular lobes. (After Ray Lankester and Bourne.)

are united by a thin supra-oesophageal commissure in the adult. The pedal centres proper supply nerves chiefly to the funnel, and thus correspond to the dorsal moieties of the pedal cords of Rhipidoglossa which innervate the epipodium; but they also send fibres to the brachial nerves, and therefore, in conjunction with the brachial ganglia, control the locomotory functions.

The pleural centres lie on the sides of the posterior part of the sub-oesophageal mass; they are but little differentiated and scarcely visible externally, and they give off the two great pallial nerves (Fig. 281, *pl*). The visceral centres are situated on the ventral side of the mass, and give off the large visceral nerves, which arise separately in *Spirula* and the Octopoda, but are more or less fused at their origin in *Ommatostrephes*, *Sepia*, etc. The pallial or "stellate" ganglia (Fig. 281, *gang.stell*) are secondary centres on the course of the pallial nerves, and are situated on the internal wall of the mantle near its anterior or dorsal border. These ganglia are connected by a transverse supra-oesophageal commissure, which is slender and is formed by the union of the two nerves of the pallial siphon in *Spirula*, is larger in sundry other Oigopsida (*Ommatostrephes*, *Onychoteuthis*, *Enoploteuthis*, *Gonatus*, *Veranya*, *Thysanoteuthis*), is reduced in *Loligo*, and is absent in the adult *Sepiola*. This commissure, together with the two fused nerves of the pallial siphon of *Spirula*, represents the two primitive pallial nerves, and is the homologue of the pallial cords, united by a commissure dorsad of the intestine, of Amphineura; whereas the large pallial nerves of the Dibranchia are neogenetic structures, evoked by the great development of the mantle borders, which are reflected over and finally enclose the shell, and give rise to the fins, etc. In some cases the visceral nerves are also united by a commissure in the form of a transverse

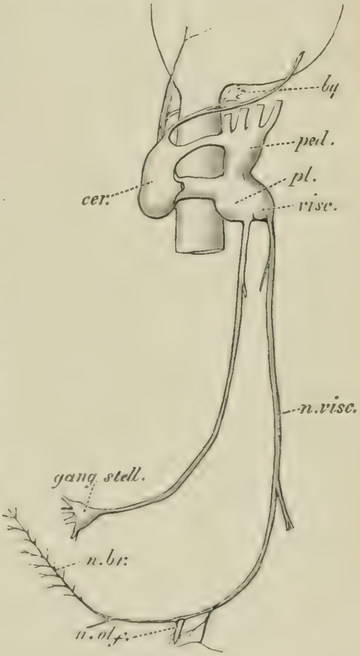


FIG. 281.

Lateral view of the nervous centres and nerves of the right side of *Octopus vulgaris*. *b.g*, buccal ganglion; *cer*, cerebral ganglion; *gang.stell*, the right "stellate" pallial ganglion; *n.br*, branchial nerve; *n.olf*, its supposed olfactory branch; *n.visc*, the right visceral nerve; *ped*, pedal ganglion; *pl*, pleural ganglion; *visc*, visceral ganglion. (After Lankester.)

bend lying near the bifurcation of the vena cava on the dorsal side of the rectum: this commissure may be seen in *Spirula* (Fig. 277, *j*), *Sepia*, and *Eledone*, and in *Ommatostrephes* it bears a large ganglion, known as the ganglion of the vena cava. In *Ommatostrephes*, *Eledone*, etc., there is yet another secondary nerve-centre at the origin of the brachial nerve.

The stomato-gastric system of the Dibranchia consists of a pair of conjoined ganglia situated below the oesophagus and immediately behind the buccal bulb (Fig. 282, XIII); these ganglia are united to the cerebrals (the anterior lobe in the Decapoda) by the intermediary of the labial commissure, as has been described above. They give off nerves to the alimentary canal, these nerves extending as far as the stomach, where they enter a large ganglion, an offshoot from which anastomoses with the visceral nerve.

The structure of the nerve-centres of the Cephalopoda resembles that of other Molluscs; they consist of a thick and continuous superficial layer of nerve ganglion cells beneath which is a fibrillar reticulum formed by the terminations of the centripetal nerve fibres and the prolongations of the superficial ganglion cells. These fibrillar centres are united by fibrillar connectives—namely, the cerebro-brachial, the cerebro-pleural, the pleuro-pedal, the pleuro-visceral, and the pleuro-brachial—many of which are short and covered over by the continuous layer of superficial ganglion cells.

The Cephalopoda are well provided with sensory organs, possessing, in addition to the tactile structures, rhinophores, statocysts, and well-developed eyes. The sense of touch is more particularly localised in the arms of the Dibranchia and the tentacles of the Tetrabranchia.

In all the Cephalopoda there is an olfactory organ situated near and below the eye on each side of the head. In sundry Oigopsida, such as *Cheiroteuthis*, *Ctenopteryx* (Fig. 259, *ol*), it is a projection, sometimes pedunculated as in *Cheiroteuthis* and *Doratopsis*; in *Nautilus* it is a cavity hollowed out in a tubercle; more generally it is a simple fossa of greater or less depth, as is the case in *Sepia* and the majority of the Dibranchia. The epithelium of this organ contains numerous sensory cells, and the nerve supplying it arises from the superior frontal lobe of the cerebral ganglion. This nerve is at first bound up with and appears to branch off from the optic nerve near a little tubercle situated on the latter, but it receives no fibres from it.

In *Nautilus* the ciliated and lamellar pre-ocular and post-ocular tentacles are apparently accessory olfactory organs; the ciliated interbranchial papilla of each side is placed on a sensorial area innervated by the fibres of the two branchiae (Fig. 280, *n.olf*). The post-anal papilla (Figs. 275, 276, *x*) is also ciliated, but is not supplied by any special nerve. In the Dibranchia the branchial ganglion of *Eledone* and *Ommatostrephes* occupies a situation analogous to that of the osphradial ganglion of Gastropoda and Lamellibranchia, but the epithelium overlying it is not sensory. It seems probable that an osphradium is not required in the Dibranchia, in consequence of the proximity of the olfactory fossa to the opening of the pallial cavity.

The statocysts or otocysts are two in number, and are always closed vesicles in adult Cephalopoda; they are essentially organs of equilibration. In *Nautilus* they are situated at the sides of the pedal centres (Fig. 279, *o*), and are closely applied to the cephalic cartilage. In the Dibranchia they are placed ventrally between the pedal and visceral centres (Fig. 282, X), and are wholly embedded in the cranial cartilage, being separated from one another only by a thin partition. The cavity of each otocyst is continued, in the Dibranchia, into a small canal which is buried in the cartilage in the Decapoda but not in the Octopoda. This canal, known as "Kölliker's canal," ends blindly, and is the remnant of the embryonic connection of the otocyst with the exterior (Fig. 119, D, *ot*). The internal wall of the otocysts of the Dibranchia is not simple, but is raised into several well-marked ridges separated by furrows. The sensory epithelium is localised at the anterior end of the organ, and forms a macula acustica, and the essential part of the otocystic nerve terminates in this macula and in a lateral ridge. The nerve originates from the cerebral ganglion and traverses the pedal centre obliquely. In *Nautilus* each otocyst contains numerous otoconia, but in the Dibranchia there is a single otolith balanced on the principal macula acustica: this otolith consists of an organic and a calcareous moiety, except in *Eledone*, in which genus it is wholly organic.

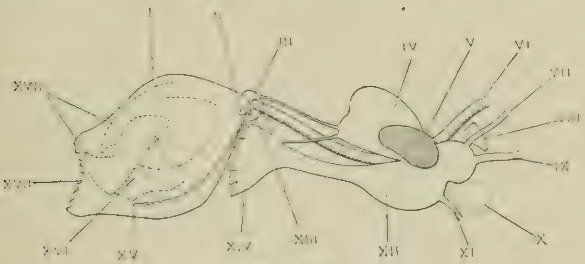


FIG. 282.

Central nervous system and anterior part of the digestive tract of *Ommatostrephes*, left-side view. I, radula; II, "anterior" salivary gland; III, anterior buccal ganglia and commissure; IV, cerebral ganglion; V, section of the optic nerve; VI, oesophagus; VII, left pallial nerve; VIII, "posterior" salivary gland; IX, visceral ganglion and nerve; X, seat of the otocysts; XI, infundibular nerve; XII, pedal ganglion; XIII, stomato-gastric ganglion; XIV, brachial ganglion and beginning of the five left brachial nerves; XV, labial commissure; XVI, "tongue"; XVII, mouth.

The eyes in all Cephalopoda are situated on the sides of the head and are generally sessile. They are, however, pedunculated in many embryos (Fig. 290, (8), (9)) and in the adult *Taonius* (Fig. 253, *e*) and other Cranchiidae, and also in some *Amphitretus* (Octopod). The eye of *Nautilus* (Fig. 293, *e*) is an open vesicle with a minute aperture (Fig. 6, A): it is devoid of any kind of refractive apparatus, and its internal retinal wall is pigmented throughout. In the Dibranchia the cavity of the eye is closed, as it is in the majority of Gastropoda, and the ocular globe consists of the same essential parts, viz. retina, cornea, and crystalline lens, with various accessory parts added, making it a very complex and perfect organ of vision. The ocular globe is applied to the cephalic cartilage, is sometimes contained in a more or less incomplete orbit formed by a wing-shaped expansion of the cartilage (*Sepia*), and is provided with a very large optic ganglion (Fig. 283, *g.o*). In the Dibranchia the retina occupies the inner part of the ocular cavity, and the rods are turned towards the light. The cornea is situated between the two segments of the cuticular body forming the crystalline lens (Fig. 283, L): above the more superficial and smaller segment of the lens a fold of the integument forms a contractile iris, with a circular (Oigopsida)

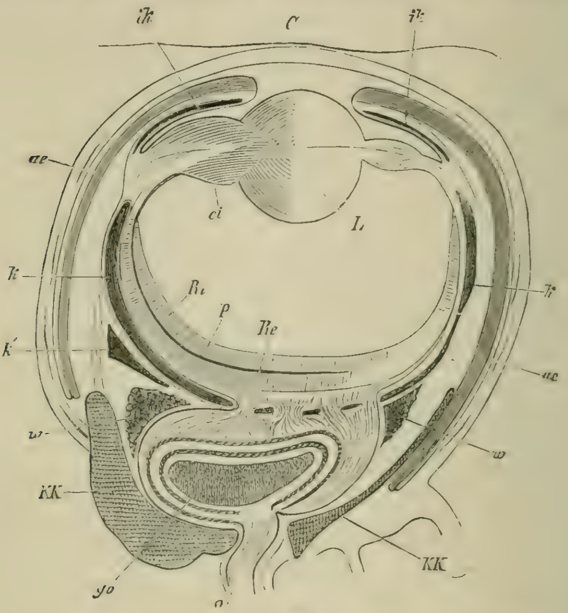


FIG. 283.

Horizontal section of the eye of *Sepia*. *ae*, argentine integument; *C*, external cornea; *ci*, ciliary body; *g.o*, optic ganglion; *ik*, cartilage of the "iris"; *k*, *k'*, capsular cartilage; *KK*, cephalic cartilage; *L*, lens; *o*, optic nerve; *P*, retinal pigment; *Re*, *Ri*, external and internal layer of the retina; *w*, white body. (From Lankester, after Hensen.)

or oval or often a reniform pupil (*Loligo*, *Sepia*, Octopoda, Fig. 288). A second more superficial fold forms an external false cornea, bounding the "anterior chamber" of the eye: the edges of this fold are not united in the Oigopsida but surround a wide orifice in the optic axis; in the rest of the Decapoda and in the Octopoda the edges of the fold unite and completely close in the anterior chamber, but in several cases a very small hole or "lacrymal pore" is left (*Sepiola*, *Sepia*). Finally, another fold, external to the false cornea, forms a transverse or inferior eyelid; this structure is best developed in the Octopoda, in which group the eye can be completely covered in by the contraction of the circular orifice of the eyelid.

The retina really consists of a single layer of cells surmounted by rods or rhabdomes, but the latter are extremely long, so that the retina is very thick. Each rhabdome is in relation to at least four retinal cells, whose prolongations extend into its interior, and each of these latter is related to two rhabdomes. A limiting layer of special cells is formed at the level where the retinal cells are joined to the rods. Below this limiting layer pigment is distributed through the retinal cells, especially in their lower ends and towards their upper extremities: in the dark all the pigment granules are collected at the bases of the cells, as in the Vertebrates and Arthropoda.

The cuticular crystalline lens is the product of both the internal and external surfaces of the true cornea. Its two segments are formed of successive concentric layers. The external segment is the less prominent of the two; the internal segment, which corresponds morphologically to the crystalline lens of Gastropoda, is much more convex and larger, but it does not occupy the whole of the ocular cavity or "posterior chamber" of the eye. The remainder of the cavity is filled by a semi-fluid vitreous body, as is the case in the majority of the Gastropoda. The eye of Dibranchia can be accommodated for near and distant vision by variation of the distance between the lens and the retina; consequently these animals are never presbyopic.

In a few genera of Cephalopods there are sensory organs which appear to be thermoscopic eyes. They are situated beneath the integument, and in *Chiroteuthis grimaldii* are found on the ventral side of the body and on the dorsal aspect of the fins. These organs consist of a large lenticular and highly pigmented chromatophore, beneath which is a flattened nerve-ending, surrounded by large transparent cells.

5. *Reproductive Apparatus.*—In all the Cephalopoda the sexes are separate, and sometimes there is a well-marked sexual dimorphism. As a rule the males are more slender (*e.g. Loligo media*) or smaller than the females, but in *Nautilus* the cephalic hood and the

aperture of the shell are wider in the male than in the female. The maximum of sexual dimorphism is found in *Argonauta*, in which genus the males are much smaller than the females: the latter may attain to fifteen times the length of the other sex, and they have an external shell and the characteristic enlargement of the dorsal arms (Fig. 301, IV), both of which features are absent in the males. Generally speaking, the males are also distinguished by the phenomenon of hectocotylisation, which consists in a curious modification for copulatory purposes of a part of the pedal circumoral crown (see p. 323).

It has been shown that the majority of the Cephalopoda are hyperpolygynous, that is to say, the males are less numerous than the females: thus in some species of *Loligo* the males are to the females as 15 : 100, in *Octopus* as 25 : 100, and in the six specimens of *Spirula* hitherto examined only one was a male. *Nautilus pompilius*, on the other hand, is hyperpolyandrous, but in *N. macromphalus* more females have been found than males. Again, in those Octopoda in which the hectocotylus is autotomous, the males appear to be more numerous, for as many as four hectocotyli have been found in the pallial cavity of a single female.

The ovary or testis of the Cephalopoda is single and median; it is situated near the aboral extremity of the body in the coelom, and is, in fact, nothing more than a projection from the wall of the latter cavity (Fig. 252, *gg*). The gonaducts open into the coelomic cavity, without being directly continuous with the gonad (Figs. 278, *o.d*, and 286, V, II); they bear accessory glands on their course (Figs. 284 and 286, I, VI, VII), and their external apertures are on the somatic wall of the pallial cavity (Figs. 275, *pc*, *l.sp*; 276, *r.ov*, *l.ov*). The male duct has no copulatory organs at its extremity, but in the Dibranchia a single arm (or two arms in *Spirula* and *Idiosepion*) and in *Nautilus* a part of the circumoral crown is modified for the purpose of fertilisation: this modification is temporary and periodic in the Dibranchia, permanent in *Nautilus*.

The females of nearly all the Oigopsida (Thysanoteuthidae, Ommatostrephidae, Onychoteuthidae, Gonatidae, etc.), and of the Octopoda with the exception of the Cirrhoteuthidae, are the only members of the Cephalopoda that preserve the primitive number of two functional and symmetrical gonaducts. In them the two oviducts originate near the same point in the genital capsule of the coelom (Fig. 278), and their external orifices are more deeply (aborally) situated in the pallial cavity in those forms in which the hectocotylus of the male is caducous. In *Nautilus* there is only a single functional gonaduct, situated on the right side, but its left homologue is always present in the form of a rudimentary duct known as the "pyriform appendage" (Lankester and Bourne), which is provided with an external orifice (Fig. 284, *Pyr*) but has no internal communication with the coelom. The artery of the pyriform sac forms a symmetrical pair with that of the right gonaduct, so that there can be no doubt as to the homology of the former organ. On the other hand, all the male Dibranchia and the females of *Spirula*, the Myopsida and the Cirrhoteuthidae, have a single gonaduct, and this always on the left side (Fig. 272, *g*).

The ovaries and testes, as well as their ducts, are strictly comparable with one another from a morphological point of view, but they differ somewhat in structural details. The ovary is simply a portion of the wall of the coelom from which the ova originate.

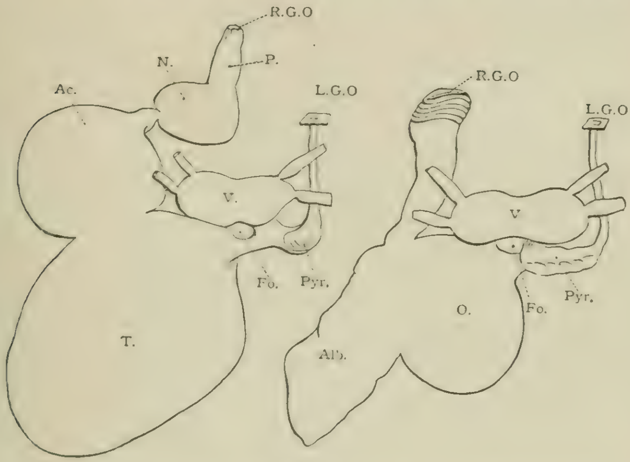


FIG. 284.

Diagrams of the male and female generative organs of the pearly *Nautilus*, to show the relation of the rudimentary duct of the left side to the testis and ovary respectively, and of the cardiac ventricle to the organs of both sides. Ventral aspect. *Ac*, accessory gland of the male apparatus; *Alb*, albuminiparous gland of the female apparatus; *Fo*, foramen in the membrane which attaches the pyriform appendage to the ventricle and to the testis or ovary (this foramen places two portions of the viscero-pericardial sac in free communication with one another): *L.G.O*, left genital orifice; *N*, Needham's sac in the male, in which the spermatophores are formed; *O*, ovary; *P*, penis; *Pyr*, Owen's pyriform appendage, attached by a membrane to the ventricle of the heart, and also to the testis or ovary; *R.G.O*, right genital orifice; *T*, testis; *V*, cardiac ventricle, with its four branchial veins. (After Ray Lankester and Bourne.)

This region generally forms a conspicuous projection, into which the coelomic epithelium is deeply invaginated in such a manner as to constitute an ovarian cavity communicating with the genital coelom by a narrow aperture. The ova that originate from the wall of this ovarian cavity are no longer superficial cells of the wall itself, but have emigrated below the ovarian epithelium, have grown in size, and have come to project into the cavity of the ovary, carrying the epithelium before them, in the same manner as the ova of many Amphineura and of *Pseudokellya*. The ova which thus lie beneath the true coelomic epithelium also become surrounded by an interior follicle formed at the expense of the cells in their neighbourhood. This follicle is nourished by an important vascular supply, and its surface of contact with the ovum is increased by the formation of equatorial and meridional folds (Fig. 285, *fo*) which penetrate into the substance of the ovum and secrete the vitellus. This vitellus forms an increasingly large part of the mass of the ovum and pushes the formative protoplasm and the nucleus up to its narrower pole opposite to the peduncle of attachment.

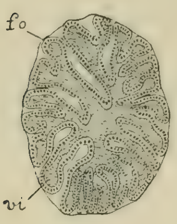


Fig. 285.

Section of an ovarian egg of *Spirula*. *fo*, ovular follicle; *vi*, vitellus. (After Huxley and Pelseneer.)

When mature the ovum acquires a chorion with a micropyle, escapes by dehiscence of its external envelope into the coelomic cavity or genital capsule (Figs. 252, *coe*; 278, *g.c*), and passes into the genital duct. In its passage through the oviduct the egg traverses a more or less voluminous glandular enlargement of the duct, situated on the wall of the genital capsule itself in *Nautilus*, at the middle of the duct in the Octopoda, near the free extremity of the duct in the Decapoda. This glandular enlargement is formed of two distinct portions in the Octopoda (Fig. 278, *o.g*) and is feebly developed in *Argonauta*, whose eggs are protected by the external shell. In addition to the true oviducal glands there are other accessory glands, unrelated to the genital ducts, in female Cephalopods. These are differentiations of the wall of the pallial cavity, and occur on the pallial wall in *Nautilus* (Fig. 270, *n*), but on the somatic wall in the Dibranchia. In the latter order they form two distinct masses, one on either side of the rectum, whereas in *Nautilus* they form a continuous mass (Fig. 276, *g.n*). In certain Oigopsida (*Enoploteuthis*, *Cranchia*, *Leachia*) and in the Octopoda these organs are absent. In the Dibranchia these "nidamentary" glands open near the genital orifice, and are generally accompanied by a second pair, as, for example, in *Sepia*: they produce the external envelopes of the eggs, formed by an elastic substance which hardens rapidly on contact with the water.

In the male, the testis is the specialised portion of the coelomic wall from which the spermatozoa are developed (Fig. 286, III): its structure is comparable with that of the ovary. The spermatozoa, when mature, pass through an orifice into the genital capsule properly so called, and thence into the spermiduct which originates from the wall of this capsule and opens externally into the pallial cavity, on the right side in *Nautilus* (Fig. 275, *pe*), on the left side in the Dibranchia (Fig. 286, VIII). Certain glandular pouches and a terminal reservoir are found on the course of the spermiduct. *Nautilus* has only one glandular pouch, but in the Dibranchia there are, as a result of specialisation, two pouches: (1) the vesicula seminalis, which is a simple enlargement; (2) the prostate.

The terminal reservoir is known as Needham's sac or the spermatophore sac (Fig. 286, VII). Between the vesicula seminalis and the prostate the spermiduct may exhibit a small tubule which opens into the coelom (*Sepia*), and in exceptional cases (*Philonexis*) the deeper part of the spermiduct may be divided into two canals, both of which open into the portion of the coelom containing the testis.

The sperm lies free in the initial part of the spermiduct, but when it reaches the first glandular pouch it begins to be surrounded by a tube-shaped envelope or spermatophore. In the Dibranchia these tubes are completed in the interior of the prostate, and are then arranged parallel to one another in the reservoir or spermatophore sac. When mature they are passed directly from the genital duct into the funnel, the terminal papilla of the spermiduct being extended for this purpose, and thus they enter the hectocotylised arm. Each spermatophore consists of an elastic tube invaginated into itself; the deeper part of the invagination constitutes the spermatic reservoir, and the more external part, forming the connective, is greatly contracted and often coiled into a spiral. When the ripe spermatophore is expelled the connective is extended and evaginated, carrying in its interior the reservoir which causes it to burst: the reservoir in its turn splits open and allows the spermatozoa contained in it to escape. These structures, which are comparable to the spermatophores of certain pulmonate Gastropods, are generally rather small; but they attain a length of eight centimetres in *Eledone*, and in the Octopoda with an autotomous hectocotylus, they are as much as fifty centimetres long when unrolled. In *Nautilus* their structure is simpler: they have the form of coiled tubes and are little more than thirty centimetres long.

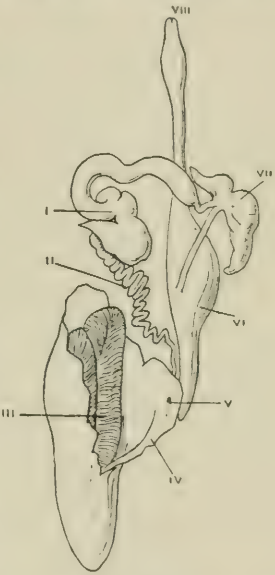


FIG. 286.

Male genital organs of *Loligo*, ventral aspect. I, seminal vesicle; II, spermiduct; III, testis; IV, genital coelomic capsule; V, origin of the spermiduct in the coelomic genital capsule; VI, spermatophore sac; VII, prostate; VIII, genital orifice. (After Duvernoy.)

The organ of copulation in *Nautilus* is the spadix, in the Dibranchia the hectocotylised arm. The spadix of *Nautilus* is a modified region—comparable with the hectocotylus—of the interior ventral lateral lobe. The modification is persistent and involves four tentacles, which are united to form a projection contained in a common sheath and provided with a circular glandular area: the eight remaining tentacles of the lobe are unaltered. The modification usually affects the left side (Fig. 255, *p*), but it has also been observed on the right. On the side opposite to the spadix the four corresponding tentacles are isolated from the other eight and constitute the so-called antispadix. In the Dibranchia the hectocotylised arm of the Decapoda generally belongs to the last pair, counting from the anterior or dorsal face, that is to say, the fourth pair of true arms, but to the third pair in the Octopoda. In the majority of the Oigopsida it is the left fourth arm that is hectocotylised (Onychoteuthidae, Ommatostrephidae), as is the case in *Loligo* and *Sepia*; in *Rossia* and *Sepiola* the fourth left arm is hectocotylised and the fourth right partially so; in *Idiosepion* and *Spirula* both arms of the fourth pair are hectocotylised, and in the last named they are contained in a common envelope. In the Octopoda the third left arm of *Scaeurgus*, the third right arm of Octopus and *Eledone*, and the second of the right side of *Cirrhoteuthis* are hectocotylised. In *Enoploteuthis*, *Eledone*, and *Octopus* the extremity of the hectocotylised arm is modified and assumes the shape of a spoon; in *Sepia* the base of the arm is affected, the modification consisting in the disappearance of the suckers; in *Idiosepion* and *Rossia* and *Loliolus* the suckers disappear over nearly the whole length of the arm, and in the two first named a longitudinal membrane is developed along its exterior aspect and abundant mucous glands along its internal surface. In some Octopoda the hectocotylised arm is still more profoundly modified, inasmuch as it is autotomous. This peculiarity is found in the Philonexidae and Argonautidae. In *Ocythoë* and *Tremoctopus* the third right arm is modified (Fig. 287, *h*), in *Argonauta* the third left; but in all these genera the modified arm constitutes a veritable hectocotylus, that is to say, a caducous organ. This hectocotylus originates, and apparently also is regenerated, in a capsule or cyst in which it lies coiled up on itself: being shielded from the light, it is

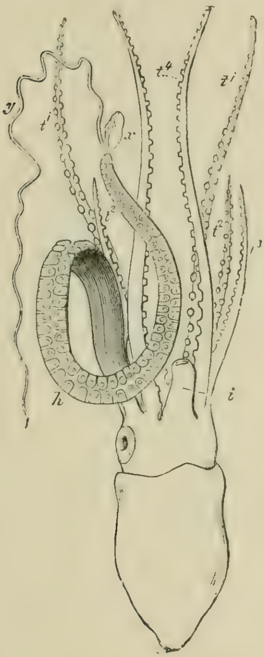


Fig. 287.

Male of *Ocythoë catenulata*, showing the hectocotylised arm, ventral view. *h*, the third arm of the right side, or hectocotylus; *i*, funnel; t^1, t^2, t^3, t^4, the first, second, third, and fourth arms; *x*, the apical sac of the hectocotylus; *y*, the filament which issues from the sac when development is complete. (From Lankester, after Gegenbaur.)

devoid of chromatophores. Eventually the membrane of the cyst bursts and remains attached to the dorsal surface of the arm, forming the spermatophore sac. The uncoiled arm is pedunculated, that is to say, is attenuated towards its base, and it bears at its extremity a little pouch (Fig. 287, *x*) containing a long filament, which is extended prior to the act of fertilisation (Fig. 287, *y*). The spermatophore sac communicates with a canal in the interior of the arm, and this canal is continued into the terminal filament and opens by an orifice at its free extremity. The hectocotylus when detached is able to live and move about for a considerable time, until finally it penetrates into the pallial cavity of a female and fixes itself in the neighbourhood of the genital aperture. In those Dibranchia in which the hectocotylus is not autotomous the hectocotylised arm (or arms) is inserted into the pallial cavity of the female (Fig. 288, 3) in such wise as to deposit the spermatophores in the terminal portion of the oviduct in *Octopus*, or to fix them in the neighbourhood of the oviducal orifice in *Rossia* and *Sepiola*. In *Sepia* and *Loligo* the spermatophores are simply deposited on the ventral lobes of the buccal membrane, and in *Nautilus* they are deposited on the folded lamellae on the ventral side of the buccal orifice (Fig. 255, *m*).

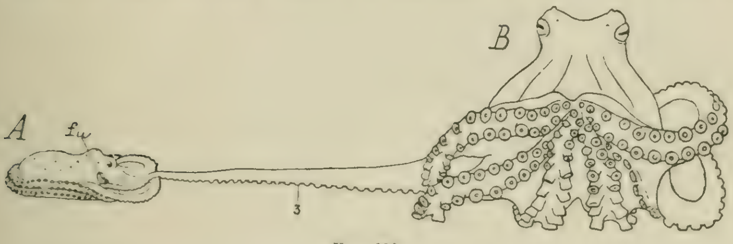


FIG. 288.

Copulation of *Octopus*. *A*, the female; *B*, the male. *fu*, funnel of the female; 3, third right hectocotylised arm of the male. (After Racovitza.)

The eggs are laid shortly after copulation. In *Nautilus* they are laid singly, each egg being about four centimetres long and surrounded by two thick shells, the outermost of which is partly open (Willey). In the Dibranchia the eggs are aggregated together, but in the Octopoda and in *Sepia*, *Sepiola*, and *Rossia* each egg has a separate envelope, whereas they are united to form longer or shorter gelatinous strings, which are joined together and fixed by one extremity in *Loligo*, but are single and floating in the pelagic Oigopsida. In *Eledone* only about sixty eggs are laid at one time, in *Octopus* more than a hundred, and some species of *Loligo* lay more than 40,000 eggs. Some Octopods are incubatory: the female *Argonauta*, for example, protects the eggs in the shell peculiar to her sex.

III. EMBRYOLOGY.

Our knowledge of the embryology of Cephalopoda is confined to the Dibranchia, the development of *Nautilus* being unfortunately still unknown. The ovum is remarkable, even in the cases of *Nautilus* and the ovarian ovum of *Spirula* (Fig. 285), for the enormous quantity of yolk contained in it. In contrast to all other Mollusca, the segmentation is incomplete: at no period does the ectoderm completely cover in the vitelline mass, so that there is no proper blastopore, or rather the blastopore is enormous and is represented by that part of the vitellus that is not covered by ectoderm (Fig. 290, (2), (3), *e*). This peculiarity in the development of Dibranchia, however, is only an exaggeration of the phenomena observable in the epibolic ova, provided with an abundant yolk, of certain Gastropoda (Fig. 10, B), and it has been shown that in the archaic Dibranchia (the Oigopsid Cephalopod of Grenacher, Fig. 119, D, *vi*) the quantity of yolk is less than in the other members of the order, and that the ectoderm extends much farther over it.

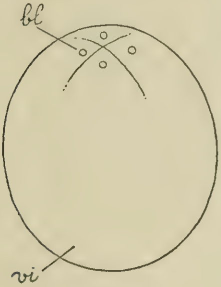


FIG. 289.

Egg of *Loligo* in the first segmentation stage. *bl*, the four first blastomeres; *vi*, vitellus. (After Watase.)

As the formative protoplasm is localised at the narrower end of the egg, the segmentation is restricted to this end (Fig. 289, *bl*), and results in the formation of a germinal disc or embryonic area. In the course of subsequent development the embryo is likewise restricted to this end, and never covers the whole surface of the vitelline mass, on which it appears to be seated (Fig. 291). The extent of the embryonic area and of the free surface of the yolk are in inverse ratio to one another: the external vitelline mass is smaller in *Loligo* than in *Sepia*, smaller still in *Argonauta*, and reduced to a minimum in the Oigopsida (Fig. 119, D).

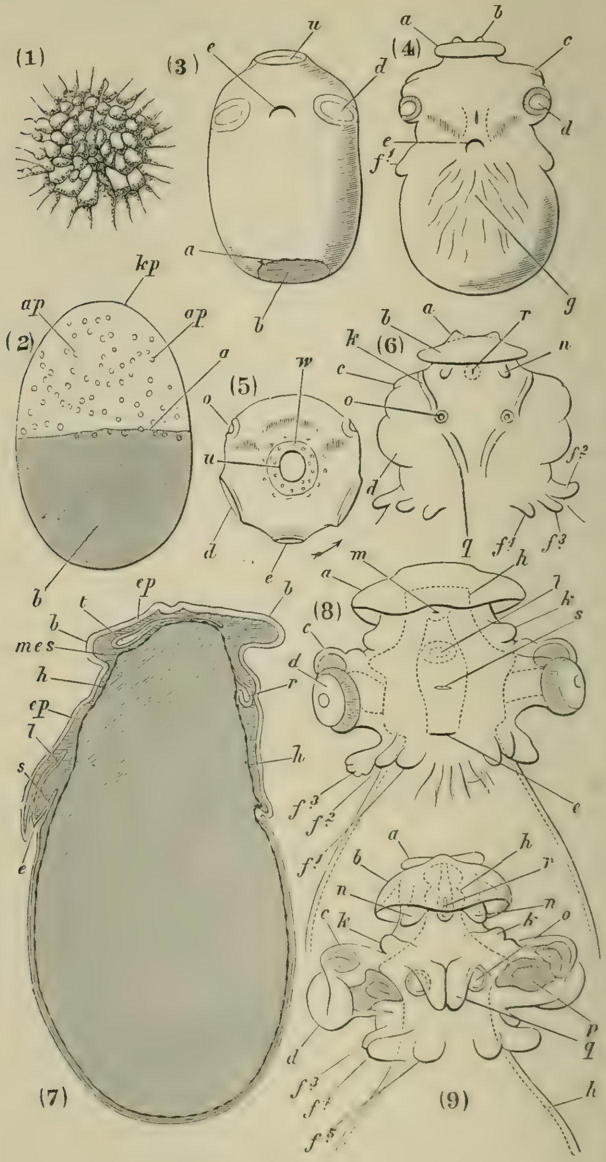
The embryonic area forms the ectoderm: the so-called perivitelline or yolk membrane is formed as a proliferation of cells from a limited part of the periphery of the ectoderm, the region of proliferation marking the anal side. The cells thus formed migrate over the whole surface of the yolk and form a layer of scattered nuclei investing it (Fig. 290, (7), *h*). At a later period the same anal edge of the periphery of the embryonic area gives rise to a second cellular layer, the endoderm: it is at first crescentic in shape, but subsequently becomes ring-shaped, and eventually forms a continuous circular sheet below the ectoderm (Teichmann). At a still later period the ectoderm gives rise to cells constituting the genital rudiment and other mesodermic elements: these cells also originate at the anal side of the blastoderm, behind the place where the shell gland is formed externally, and extend in the form of a crescent, right and left, between the ectoderm and endoderm, toward the anterior part of the blastoderm. After the mesoderm has been established in this manner, a thickened specialised portion of the endoderm constitutes the rudiment of the mesenteron and forms a little vesicle lying close upon and widely open to the yolk, and situated in the middle line, below the posterior part of the mantle, between the rudiments of the two branchiae (Fig. 290, (6), *r*). This vesicle is the rudiment of the alimentary tract: it ultimately gives rise to the stomach, the two lobes of the liver (which are separate from the first), and the intestine (Fig. 290, *r*).

The oesophagus and its annexes, viz. the radula, the salivary glands, etc. (Fig. 290, (7), *l*, *s*), are formed by a precocious stomodaeal invagination, and the anus is formed later, by an excessively short proctodaeal invagination. Thus the mouth arises relatively near to the nutritive or vegetative pole, as it does in other Mollusca, and the less abundant the yolk, the nearer it is to the vegetative pole, as in the Cephalopod of Grenacher (Fig. 119, D).

The mantle arises in the middle of the embryonic area (Fig. 257, *pa*), and in its centre is the shell gland, but the borders of the latter structure are reflected inwards and approach one another to form the shell sac. In certain highly differentiated Octopoda (*Argonauta*, Ray Lankester) the shell sac disappears before it is closed up, but in the Decapoda, with the exception of *Spirula*, it is completely closed, and it grows *pari passu* with the mantle (Fig. 290, *t*), while the shell develops within it. Posteriorly to the mantle, between it and the epipodium, appear the bud-like rudiments of the branchiae (Fig. 290, (6), *n*), and the folds that form the branchial lamellae gradually make their appearance and become in their turn folded. As development advances the pallial cavity becomes deeper, and the branchiae are gradually covered by the mantle.

Throughout the earlier part of embryonic life the cephalic mass is excessively large (Fig. 290, (8), (9)), but its preponderance insensibly diminishes in subsequent stages. This cephalic mass is formed by the antero-lateral regions of the embryonic area, and it bears the rudiment of an eye at each posterior corner (Fig. 290, (9), *d*).

During these earlier phases of embryonic development the mouth is not in any sense surrounded by the circumoral appendages. The foot, in fact, is at first formed by the lateral and posterior borders (Fig. 257, 1, 2, 3, 4, 5) of the embryonic area, and these borders are rapidly divided into ten projections in the Decapoda, or eight projections in the Octopoda and the Cephalopod of Grenacher (Fig. 119, D). But in the course of development these lobes, while they grow in length, also advance gradually


(1)
(3)
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u
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h

Fig. 290.

along the sides until the most anterior of them reach the mouth (Fig. 291), and becoming united in front of it, eventually surround it completely.

A paired epipodial outgrowth, the origin of the funnel, is formed early in development: its two posterior lobes become prominent and bend inwards toward one another (Fig. 290, *q*), thus establishing the condition which is permanent in the adult *Nautilus* (Fig. 276), but finally, in the Dibranchia, they fuse together completely and form a perfect tube.

All the nervous centres—the cerebral, optic, visceral, and pedal—are formed separately as proliferations of the ectoderm. The pedal centres give rise, by subdivision, to the ganglia of the arms. The eyes (Fig. 292, A, B) and otocysts originate as invaginations of the ectoderm, which eventually close up. The otocysts arise laterally on the sides of the foot outside the epipodium (Fig. 290, (6), *o*); they close up at a relatively late period, often retaining a rudiment of the original external canal, and then approach one another till they come in contact in the median line. When the ocular cavity is closed, the external part of the crystalline lens is formed separately from the internal segment. At the sides of the optic ganglia a pair of cellular masses, formed by ectodermic invaginations, becomes the white bodies of the adult (Fig. 290, *c*); they are the relics of a pair of embryonic ganglia (lateral cerebral lobes).

FIG. 290.

Development of *Loligo*. (1) view of the cleavage of the egg during the first formation of embryonic cells. (2) lateral view of the egg at a little later stage; *a*, limit to which the layer of cleavage-cells has spread over the egg; *b*, portion of the egg as yet uncovered by cleavage-cells; *ap*, yolk membrane cells; *kp*, cleavage-pole where first cells were formed. (3) later stage, the limit *a* now extended so as to leave but little of the egg-surface (*b*) unenclosed; *d*, eyes; *e*, mouth; *u*, mantle sac. (4) later stage, anterior surface, the embryo is becoming nipped off from the yolk sac (*g*). (5) view of an embryo similar to (3) from the cleavage-pole or centro-dorsal area. (6) later stage, posterior surface. (7) section in a median sagittal plane of an embryo of the same age as (4). (8) view of the anterior face of an older embryo. (9) view of the posterior face of an embryo of the same age as (8). Letters in (3) to (9):—*a*, lateral fins; *b*, mantle-skirt; *c*, supra-ocular invagination to form the "white body"; *d*, the eye; *e*, the mouth; *ep*, outer layer of the embryo; f^1, f^2, f^3, f^4, f^5, the five paired processes (arms) of the foot; *g*, rhythmically contractile area of the yolk sac; *h*, dotted line showing internal area occupied by yolk; *k*, first rudiment of the funnel; *l*, sac of the radula; *m*, stomach; *mes*, mesoderm; *n*, rudiments of the gills; *o*, the otocysts; *p*, optic ganglion; *q*, distal portion of the ridges which form the funnel; *r*, vesicle-like rudiment of the intestine formed independently of the parts connected with the mouth; *s*, rudiment of the salivary gland; *t*, the closed shell sac; *u*, the open shell sac, formed by an uprising ring-like growth of the central dorsal area; *w*, the mantle-skirt commencing to be raised up around the area of the shell sac. (After Lankester.)

The coelomic cavity is hollowed out in the mesoderm as two symmetrical spaces, right and left of the intestine; it gives rise to the kidneys and the pericardium. The two kidneys are formed independently of one another in their definitive positions. The heart is also formed from the pericardial wall as two paired rudiments. Finally, a portion of the coelomic wall gives rise to the gonad.

The vitelline mass diminishes insensibly during the growth of the embryo, and is for the most part absorbed at the time of hatching. The yolk sac is independent of the stomach, and is only in contact with it over a small area in the middle line.

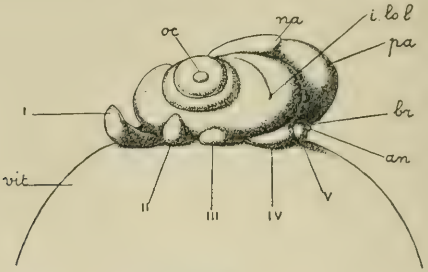

FIG. 291.

Embryo of *Sepia officinalis*, on its vitellus, left-side view. *an*, anus; *br*, gill; *i.lo.l*, invagination of the lateral cerebral lobe; *na*, fin; *pa*, mantle; *vit*, vitellus. I, II, III, IV, V, the five left arms.

IV. BIONOMICS AND DISTRIBUTION.

All the Cephalopoda are marine, and very active animals. They swim rapidly by expelling the water from the pallial cavity through the funnel, sometimes with so much violence that they can spring for some distance out of the water (*Ommatostrephes*). The fins of the Dibranchia are organs of balance rather than of locomotion. All the Cephalopods are in the highest degree carnivorous: many of them destroy a large number of edible fish and Crustacea, but, on the other hand, many of the pelagic forms fall a prey to the toothed whales.

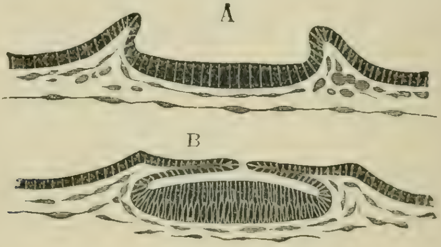

FIG. 292.

Diagrams of sections showing the early stage of development of the eye of *Loligo*, when it is, like the permanent eye of *Nautilus*, an open sac. *A*, first appearance of the eye as a ring-like upgrowth; *B*, ingrowth of the ring-like wall so as to form a sac, the primitive optic vesicle. (After Lankester.)

Some Cephalopods attain to a very considerable size: the body of some species of *Architeuthis*, without the head, may measure two and a half metres in length, and when the head and extended tentacular arms are taken into account, they may be from twelve to eighteen metres long. Hence these Mollusca have given rise to various fabulous tales, and they have been known by man from the remotest periods of antiquity, as is evidenced by their representations on some of the most ancient monuments from Mycenae, Egypt, and Greece.

In the present day some four hundred species of Cephalopoda are distributed throughout all the seas of the world. Some species, especially those with a short and rounded pallial sac, such as the Octopodidae and *Sepiola*, are strictly littoral—indeed *Sepiola* and also *Rossia* are fossorial in habit. Other species are inhabitants of the open sea, and among these various forms of Oigopsida dwell in great depths: *Spirula* is found down to 1000 fathoms; *Cranchia* and *Bathyteuthis* down to 1700 fathoms; *Histiopsis* at a depth of nearly 2000 fathoms; *Calliteuthis* at 2200; and *Cheiroteuthis* down to 2600 fathoms. Many of these deep-sea Oigopsida are luminous.

The history of the Cephalopoda extends back to the remotest geological times. *Orthoceras* and other forms allied to *Nautilus*, but as yet uncoiled, are abundant in the most primitive Palaeozoic formations. The subdivision of the Ammonitoidea, related to the Tetrabranchia, is distributed from the Devonian to the end of the Secondary period. The Dibranchia do not appear till the end of the Secondary epoch, during which they were characteristically represented by the Belemnitidae, a group which, like the Ammonitoidea, became nearly completely extinct at the end of this period.

V. REVIEW OF THE ORDERS, SUB-ORDERS, AND FAMILIES OF THE CEPHALOPODA.

The class Cephalopoda comprises two orders, the Tetrabranchia and the Dibranchia. Palaeontology, as well as morphology, shows that the Tetrabranchia (*Nautilus*, etc.), that is to say, the Cephalopods with multiple branchiae, auricles, and kidneys, and with an external chambered shell, are the most archaic. The Dibranchia are more specialised, inasmuch as they have lost the anterior branchiae, auricles, and kidneys, and their shell has become rudimentary. The earliest Dibranchia were descended from rectilinear forms with a multilocular external shell devoid of a rostrum, and they gave rise in turn to *Spirula*, the Belemnitidae, and the allied Oigopsida. From the last named were derived, as the result of a yet more profound specialisation, on the one hand the Myopsida, on the other hand the Octopoda, by the loss of the tentacular arms (already so much reduced as to be almost lost in some Oigopsida), and by the more and more complete atrophy of the shell.

Order 1. **Tetrabranchia**, Owen.

In these Cephalopoda the whole of the visceral mass is protected by an external, multilocular, siphunculated shell, which may or may not be coiled; only the last compartment of the shell is occupied by the body of the animal. The head bears numerous appendages in the form of pedal tentacles, which are retractile within sheaths (Fig. 293, *te*). The funnel is formed of two separate moieties. There are four branchiae, and four kidneys without reno-pericardial orifices. The pericardium opens directly to the exterior. The cephalic cartilage is wholly situated on the ventral side of the oesophagus (Fig. 270, *h*) and only supports the ventral part of the nervous centres. The eyes are open and have no crystalline lens (Fig. 6, A). The Tetrabranchia comprise two sub-orders, the Nautiloidea and the Ammonitoidea.

Sub-Order 1. Nautiloidea.

This group is distinguished from the Ammonitoidea by the initial chamber, which is in the form of an obtuse cone bearing on its summit a "cicatrix," elongated dorso-ventrally and situated opposite the extremity of the blind end of the siphuncle: it is probable that the siphuncle passed through this cicatrix on emerging from a true initial chamber or protoconch, which may have been uncalcified or caducous. The sub-order comprises nearly 2500 fossil species, but only a few living species of the genus *Nautilus*. In certain fossil forms the aperture of the shell may be contracted to such an extent that the animal was probably able to protrude only the appendages of the circumoral crown, but not its head. These contracted apertures are said to be "composite" when they have lobes of different form, as in *Gomphoceras*, *Phragmoceras*, etc. In these apertures the ventral part, corresponding to the funnel, is separated from the rest by a constriction, and constitutes the "hyponomous sinus"; the remainder of the aperture is more or less lobate and corresponds to the external parts of the circumoral crown. The shell may attain to a length of two metres (*Endoceras*).

Family 1. Orthoceratidae. Shell straight or slightly curved, with a simple aperture, a large terminal chamber, and a cylindrical siphuncle. Genera—*Orthoceras*, Breyn; from the Silurian to the Trias. *Baltoceras*, Holm; Silurian. Family 2. Actinoceratidae. Shell straight or slightly curved, with a wide siphuncle contracted at the level of the septa by rings or swellings. Genera—*Actinoceras*, Bronn; from the Silurian to the Carboniferous. *Discosorus*, Hall; Silurian. *Huronia*, Stokes; Silurian. *Loxoceras*, MacCoy; from the Silurian to the Carboniferous. Family 3. Endoceratidae. Shell straight, with a wide marginal siphuncle, the siphuncular necks produced into tubes which fit into one another. Genera—*Endoceras*, Hall; shell straight; from the Silurian. Family 4. Gomphoceratidae. Shell globular, straight or arcuate, the aperture contracted to the shape of a T. Genera—*Gomphoceras*, Sowerby; Silurian. *Phragmoceras*, Sowerby; Silurian. Family 5.

ASCOCERATIDAE. Shell straight, ampulliform; the summit truncated; the terminal chamber occupies nearly the whole length of the shell on the ventral side. Genera—*Ascoceras*, Barrande; Silurian. *Glossoceras*, Barrande; Silurian. FAMILY 6. POTERIOCERATIDAE. Shell straight or curved, fusiform, contracted at the two extremities; the aperture simple; the siphuncle contracted at the levels of the septa. Genera—*Poterioceras*, MacCoy; from the Silurian to the Carboniferous. *Streptoceras*, Billings; Silurian. FAMILY 7. CYRTOCERATIDAE. Shell slightly curved; the aperture simple; the siphuncle wide and the septa approximated. Genus—*Cyrtoceras*, Goldfuss; Devonian. FAMILY 8. LITUITIDAE. Shell coiled in one plane with the terminal part uncoiled; the aperture contracted. Genera—*Lituites*, Barrande; Silurian. *Ophidioceras*, Barrande; Silurian (Fig. 261, A). FAMILY 9. TROCHOCERATIDAE. Shell helicoidally coiled; dextral or sinistral; the last whorl generally uncoiled. Genera—*Trochoceras*, Barrande; Devonian. *Adelphoceras*, Barrande; Devonian. FAMILY 10. NAUTILIDAE. Shell coiled in one plane; the aperture wide and simple; the siphuncle central. Genera—*Nautilus*, Linnaeus (Figs. 270 and 293); four living species are known from the Indian and Pacific Oceans: they are gregarious, nocturnal animals, living at some depth. *Trocholites*, Conrad; Silurian. *Gyroceras*, de Koninck; from the Silurian to the Carboniferous. *Hercoceras*, Barrande; Silurian. *Ptenoceras*, Hyatt; Devonian (Fig. 261, B). *Discites*, MacCoy; Carboniferous. FAMILY 11. BACTRITIDAE. Shell straight, conical; the siphuncle narrow and marginal, and the siphuncular necks long and infundibuliform; septa united to the shell by an undulating line. Genus—*Bactrites*, Sandberger; Silurian and Devonian.

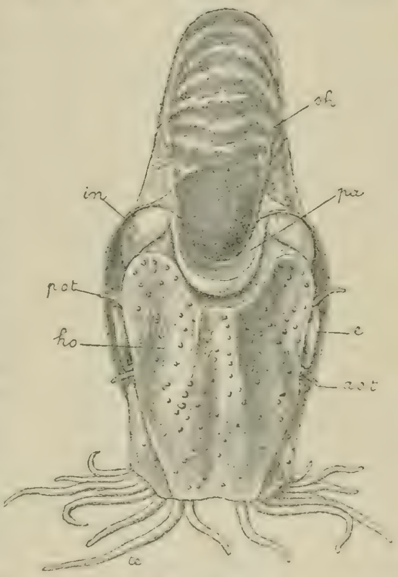

FIG. 293.

Nautilus macromphalus creeping on a horizontal surface, anterior view. *a.o.t*, anterior ophthalmic tentacle; *e*, eye; *ho*, hood; *in*, infundibulum; *pt*, nuchal part of the mantle; *p.o.t*, posterior ophthalmic tentacle; *sh*, shell. (After Willey.)

SUB-ORDER 2. AMMONITOIDEA.

The Ammonitoidea are distinguished from the Nautiloidea by their initial chamber, which is spheroidal like that of the Belemnitidae and Spirulidae; by their siphuncle, which is narrow and simple, whereas that of the Nautiloidea is wide, but often reduced in diameter by internal deposits; by their septa, which are generally convex on the side nearer the aperture, instead of being concave as in the Nautiloidea; finally, by the sutures (intersections of the septa with the shell), which form a more or less complex sinuous line, instead of being simple as in the Nautiloidea.

Although the Ammonitoidea have a globular initial chamber which is absent in Nautiloidea (though it may possibly be present but caducous or not calcified in the latter group), their shell has the same structure as that of *Nautilus*, and was indisputably external. The chamber containing the body of the animal is very deep, more so than in *Nautilus*. Like the Nautiloidea, the Ammonitoidea did not possess an ink-sac. A considerable number of Ammonitoidea resemble such Nautiloid forms as *Gomphoceras*, *Phragmoceras*, etc., in having a contracted aperture, indicating an analogous structure of the cephalopedal organs: such contracted apertures may be seen in *Arcestes*, *Lobites*, *Stoliczkaia*, and especially in *Stephanoceras*, but this contraction is carried to an extreme in *Morphoceras pseudoanceps* (Fig. 294). In this genus the aperture is almost completely closed by the lobes which form its borders and circumscribe five small orifices; there is a central oblong orifice which probably corresponded to the mouth; two circular lateral orifices, one on either side of the central, may perhaps have served as windows for the eyes; and the two remaining orifices, which are partly limited by the preceding whorl, probably served for the passage of the pedal appendages, and do not correspond to any part of the contracted apertures of Nautiloidea. A calcified structure, consisting of a single piece (Anaptychus) or of two symmetrical moieties (Aptychus) is sometimes found in the terminal chamber of Ammonitoidea: its constant position shows that it could not have been an operculum, and it is supposed to have been a calcified cartilage situated at the base of the funnel.

The Ammonitoidea are, geologically speaking, younger than the rest of the Tetrabranchia. They appeared in the Devonian and became completely extinct at the end of the Secondary period. They were littoral in habit, and lived in troops like *Nautilus*. Some of the coiled forms are as much as seventy centimetres in diameter. More than 5000 species have been described, and it has been found necessary to divide the originally single genus *Ammonites* first into genera, then into families, and even into tribes.

TRIBE 1. RETROSIPHONATA.

The siphuncular necks project behind the septa as in the Nautiloidea. These are the most ancient Ammonitoidea, belonging exclusively to the superior Palaeozoic strata, from the Devonian upwards. The sutures of the septa form simple undulations, those which point backwards being known as "lobes," and those which point forward towards the aperture as "saddles."

FAMILY 1. GONIATITIDAE. Shell nautiloid with simple sutures and a ventral siphuncle. Genera—*Goniatites*, de Haan; Devonian and Carboniferous. *Anarcestes*, Mojsisovics; Devonian. FAMILY 2. CLYMENIIDAE. Shell nautiloid; sutures simple; the siphuncle dorsal, that is to say, internal. Genus—*Clymenia*, Münster; from the Upper Devonian.

TRIBE 2. PROSIPHONATA.

The siphuncular necks project in front of the septa. The septal sutures present deeply indented lobes and saddles.

FAMILY 1. ARCESTIDAE. Globular and smooth or nearly smooth forms, with a reduced umbilicus; the terminal chamber very deep, occupying nearly a whole whorl of the spire; an aptychus present. Genera — *Popanoceras*, Gemmellaro; Permian. *Cyclolobus*, Waagen; Permian. *Arcestes*, Mojsisovics; Trias. *Lobites*, Mojsisovics; Trias. FAMILY 2. TROPITIDAE. The shells globular, but differing from those of the Arcestidae in having radiating and tuberculated costae. Genera—*Thalassoceras*, Gemmellaro; Permian. *Tropites*, Mojsisovics; Trias. *Sibirites*, Mojsisovics; Trias. FAMILY 3. CERATITIDAE. Shells coiled, with a large umbilicus; the terminal chamber short; sutures with simple saddles. Genera—*Trachyceras*, Laube; Upper Trias. *Ceratites*, de Haan; Trias. *Dinarites*, Mojsisovics; Trias. Some genera with helicoidal shells are related to these coiled forms, viz. *Cochloceras*, Hauer; Trias: also some straight forms, *e.g.* *Rhabdoceras*, Hauer; Trias: they have been placed in distinct families by some authors. FAMILY 4. PINACOCERATIDAE. Shell compressed, smooth; the terminal chamber short; the suture very complicated, convex. Genus — *Pinacoceras*, Mojsisovics; Trias. FAMILY 5. PHYLLOCERATIDAE. Shells coiled, the whorls overlapping one another; the suture formed of numerous lobes and saddles. Genera — *Phylloceras*, Suess; Jurassic. *Rhacophyllites*, Zittel. FAMILY 6. LYTOCERATIDAE. Shell discoid, the whorls loosely united or uncoiled; the sutures deeply indented but with only three saddles and lobes. Genera—*Lytoceras*, Suess; Jurassic and Cretaceous. *Macroscaphites*, Meek; uncoiled and recurved; Cretaceous. *Hamites*, Parkinson; flexed three times; Cretaceous. *Ptychoceras*, d'Orbigny; Cretaceous. *Turrilites*, Lamarck; coiled in a sinistral helicoidal spire; Cretaceous. *Baculites*, Lamarck; the adult straight and elliptic in section; Cretaceous. FAMILY 7. AMMONITIDAE. Shell coiled, with narrow whorls which do not embrace one another; aperture simple; a horny anaptychus present. Genera—*Ammonites*, Lamarck; Jurassic. *Arietites*, Waagen; Jurassic. *Aegoceras*, Waagen, Lias. FAMILY 8. HARPOCERATIDAE. Shell discoid and flattened, with a carinated border; the aperture provided with lateral projections; a calcareous aptychus, formed of two pieces. Genera—*Harpoceras*, Waagen; Jurassic. *Oppelia*, Waagen; Jurassic. *Lissoceras*, Bayle; Jurassic and Cretaceous. FAMILY 9. AMALTHEIDAE. Shell flattened, with a prominent carina continued anteriorly into a rostrum. Genera—*Amaltheus*, Montfort; Lias. *Cardioceras*, Neumayr; Jurassic. *Schloenbachia*, Neumayr; Cretaceous. FAMILY 10. STEPHANOCERATIDAE. Shell not carinated, but with radiating costae, which are often bifurcated; aperture often provided with lateral pro-

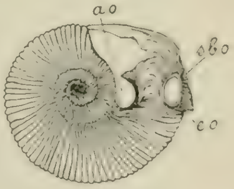

FIG. 294.

Morphoceras pseudoanceps, right-side view. *a.o*, orifice for arms; *e.o*, eye-orifice; *s.b.o*, infundibulo-buccal orifice. (After Douvillé.)

jections which contract it; aptychus formed of two pieces. Genera—*Stephanoceras*, Waagen; Jurassic. *Morphoceras*, Douvillé; Jurassic (Fig. 294). *Perisphinctes*, Waagen; Jurassic. *Peltoceras*, Waagen; Jurassic. *Hoplites*, Neumayr; Cretaceous. *Acanthoceras*, Neumayr; Cretaceous. *Cosmoceras*, Waagen; Jurassic. Various more or less completely uncoiled forms are related to this family, viz. *Scaphites*, Parkinson; Cretaceous. *Crioceras*, d'Orbigny; Cretaceous.

ORDER 2. **Dibranchia**, Owen.

In these Cephalopoda the external surface of the visceral mass is naked and is only protected by a more or less rudimentary shell, which is situated on the aboral surface and covered by the integuments of this region. The female *Argonauta* is the only member of the group that has a wholly external shell, but this is not adherent and is secreted by the dorsal arms. The head of the Dibranchia bears eight acetabuliferous arms, and there is frequently a fifth pair of more or less retractile arms, situated between the third and fourth pair (Fig. 295, *te*). The funnel is always a completely closed tube (Figs. 287, 301, etc.). There are two branchiae and two kidneys, each of the latter having a pericardial orifice (Fig. 273, *y*). The cephalic cartilage is traversed by the oesophagus and encloses all the principal nervous centres. The ocular cavities are closed and the eyes have a crystalline lens (Fig. 283). Chromatophores are present in the integument and an ink-sac is generally present. The Dibranchia include two sub-orders, the Decapoda and the Octopoda.

SUB-ORDER 1. DECAPODA.

In this sub-order, in addition to the eight pairs of normal arms, there is a more or less well developed "tentacular" arm situated between the third and fourth normal arms, on each side of the head. These tentacular arms are more or less retractile within special pouches, and as a rule they only bear suckers at their free extremities. The suckers are pedunculated and provided with horny rings. The eight normal arms are shorter than the body. There is generally a fairly well developed internal shell, and there are usually lateral fins of various width (Figs. 295, 296, etc., *fi*). The heart lies in a coelomic cavity. Nidamentary glands are usually present.

The Decapoda comprise two tribes, the Oigopsida and the Myopsida.

TRIBE 1. OIGOPSIDA.

The members of this tribe are characterised by the presence of a wide orifice, occupying the optic axis, in the external false cornea of the eye. As a rule two oviducts are present. In the fossil genera the shell has a multilocular phragmocone with a siphuncle; the initial chamber of this shell is globular and larger than the second chamber. The most ancient forms are characterised by the small size of the rostrum, the slight development of the pro-ostracum, and the large size of the phragmocone. The group is probably derived from the straight Tetrabranchia, such as *Bactrites.* In the living genera, with the exception of *Spirula*, the shell is a chitinous gladius.

FAMILY 1. BELEMNOTEUTHIDAE, Zittel. An extinct family in which the shell has a well-developed phragmocone and the rostrum is reduced to a calcareous envelope surrounding it; the siphuncular necks are directed backwards, as in the Nautiloidea; there were ten equal arms provided with hooks. Genera—*Phragmoteuthis*, Mojsisovics; Trias. *Belemnoteuthis*, Pearce; Jurassic and Cretaceous (Fig. 262, A). *Acanthoteuthis*, Wagner and Münster; Jurassic. FAMILY 2. AULACOCERATIDAE, Fischer. An extinct family in which the shell is formed of a phragmocone with widely distant septa; the siphuncular necks are directed anteriorly; the rostrum is well developed and claviform. Genera—*Aulacoceras*, Hauer; Trias. *Atractites*, Gümbel; Trias and Jurassic. *Xiphoteuthis*, Huxley; Lias. FAMILY 3. BELEMNITIDAE, de Blainville. An extinct family with a short phragmocone provided with a ventral siphuncle and prolonged dorsally into a long pro-ostracum; the rostrum highly developed and cylindrical. Genera—*Belemnites*, Lister; 350 species from the Jurassic and Cretaceous. *Diploconus*, Zittel; Upper Jurassic. FAMILY 4. BELOPTERIDAE. Rostrum and phragmocone well developed; the phragmocone often curved; the initial chamber small. Genera—*Beloptera*, de Blainville; Eocene. *Bayanoteuthis*, Munier-Chalmas; Eocene. *Spirulirostra*, d'Orbigny; Miocene (Fig. 262, C). FAMILY 5. SPIRULIDAE, d'Orbigny. The two dorsal and ventral sides of the aboral

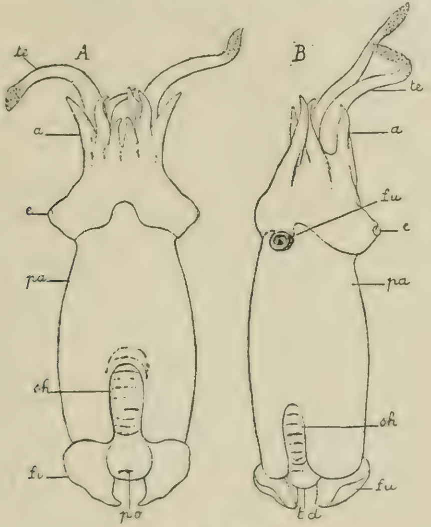

FIG. 295.

Spirula. *A*, dorsal aspect; *B*, ventral aspect. *a*, arms, *e*, eyes; *fi*, fins; *fu*, funnel; *pa*, mantle; *po*, posterior fossa; *sh*, shell; *te*, tentacular arms; *t.d*, terminal pallial disc. (After Chun.)

extremity of the shell are left uncovered by the mantle (Fig. 295). The shell is calcareous, coiled endogastrically, multilocular and siphunculated (Fig. 268, *sh*). The fins are posterior. Genus—*Spirula*, Lamarck ; three living species are known ; they live at great depths, and only a few entire individuals have been obtained : live specimens are very rarely seen. FAMILY 6. OMMATOSTREPHIDAE, Gill. The shell is internal and chitinous, ending aborally in a little hollow cone. The tentacular arms are rather short and thick. The suckers have denticulate rings. Genera—*Ommatostrephes*, d'Orbigny ; fins aboral, simple, and rhomboidal (Fig. 297) ; British. *Ctenopteryx*, Appellöf ; fins pectinate, as long as the body (Fig. 259). *Bathyteuthis*, Hoyle ; fins terminal, rudimentary ; tentacular arms filiform ; abyssal. *Rhynchoteuthis*, Chun ; tentacular arms united to form a beak-shaped appendage. *Symplectoteuthis*, Pfeiffer. *Trachelo-teuthis*, Steenstrup. *Dosidicus*, Steenstrup. *Architeuthis*, Steenstrup ; this is the giant genus among the Cephalopoda. FAMILY 7. THYSANOTEUTHIDAE,

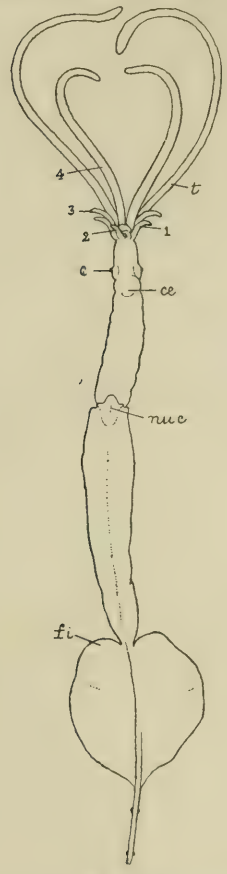

FIG. 296.

Doratopsis vermicularis (Rüppel), dorsal aspect. *ce*, cerebral ganglia ; *e*, eye ; *fi*, fin ; *nu.c*, nuchal cartilage ; *t*, tentacular arm ; 1, 2, 3, 4, pair of arms. (After Weiss.)

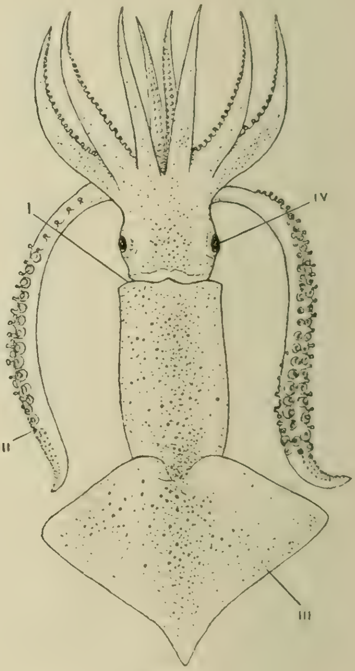

FIG. 297.

Ommatostrephes sagittatus, Lamarck, dorsal aspect. I, mantle ; II, tentacular arm ; III, fin ; IV, eye ; V, arms. (After Verany.)

Keferstein. Arms enlarged, bearing two rows of suckers and filaments. Fins triangular, extending along the whole length of the body. Genus—*Thysanoteuthis*, Troschel (Fig. 298, B); Mediterranean. FAMILY 8. ONYCHOTEUTHIDAE, Gray. Fins terminal. Tentacular arms long; the suckers provided with hooks. Genera—*Onychoteuthis*, Lichtenstein; the hook-bearing suckers exist only on the well-developed tentacular arms. *Enoploteuthis*, d'Orbigny; tentacular arms well developed; hook-bearing suckers on all the arms. *Veranya*, Krohn; body very short; fins obtuse; tentacular arms atrophied in the adult; Mediterranean. *Chaunoteuthis*, Appellöf; body elongated; fins prominent and pointed; tentacular arms atrophied. *Pterygioteuthis*, Fischer. *Ancistroteuthis*, Gray. *Abralia*, Gray. *Teleoteuthis*, Verrill. *Lepidoteuthis*, Joubin. FAMILY 9. GONATIDAE, Hoyle. Body elongated; fins terminal. Radula with only two lateral teeth. Genus—*Gonatus*, Gray. FAMILY 10. CHEIROTEUTHIDAE, Gray. Tentacular arms long and not retractile. Body elongated; fins large and rounded. Resisting apparatus well developed. Genera—

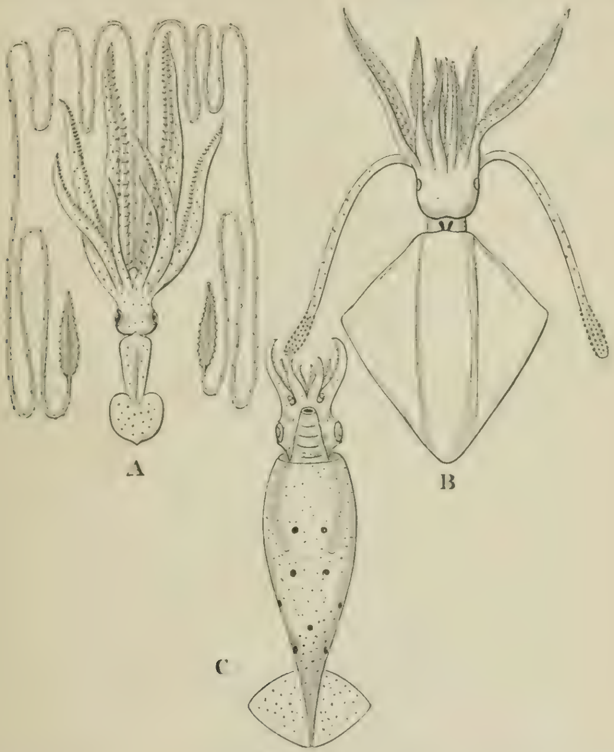

FIG. 298.

Decapod Cephalopoda. *A*, *Cheiroteuthis Veranyi*, dorsal aspect; *B*, *Thysanoteuthis rhombus*, dorsal aspect; *C*, *Leachia cyclura*, ventral aspect. (From Lankester, after Verany, Troschel, Férussac and d'Orbigny.)

Cheiroteuthis, d'Orbigny ; with suckers along the whole length of the peduncle of the tentacular arms (Fig. 298, A). *Doratopsis*, Rochebrune ; body much elongated, ending in a spine ; dorsal arms very short (Fig. 296) ; Atlantic and Mediterranean. *Histioteuthis*, d'Orbigny ; the six dorsal arms are united by a membrane ; the body covered with photogenous organs. *Histiopsis*, Hoyle ; the membrane of the dorsal arms only reaches half-way up the arms ; luminous organs present. *Calliteuthis*, Verrill ; no brachial membrane ; luminous organs present. *Grimalditeuthis*, Joubin ; the fin of each side is divided into two separate lobes : no tentacular arms (Fig. 258). FAMILY 11. CRANCHIIDAE, Gray. The eight normal arms are very short. The eyes prominent. The fins small and terminal. Genera—*Cranchia*, Leach ; body bursiform ; sessile arms short ; fins entirely aboral. *Loligopsis*, Lamarck ; body elongated, conical ; tentacular arms slender. *Leachia*, Lesueur ; tentacular arms aborted ; the funnel without a valve (Fig. 298, C). *Taonius*, Steenstrup ; body elongate ; sessile arms rather short ; eyes pedunculated (Fig. 253).

TRIBE 2. MYOPSIDA.

The members of this tribe are characterised by having a closed external cornea, and by having only a single oviduct, viz. that of the left side. The internal shell has no longer a distinct phragmocone, and is calcified (Sepiidae) or simply chitinous. The Myopsida are more littoral in habit than the Oigopsida.

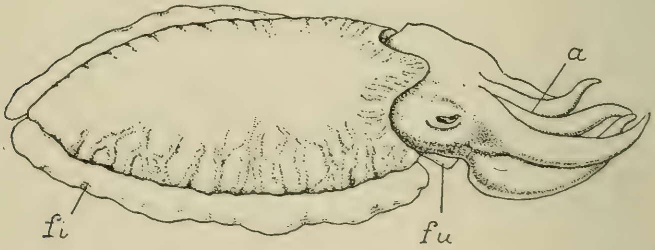

FIG. 298^{bis}.

Sepia officinalis, swimming, right-side view. *a*, arms ; *fi*, fins ; *fu*, funnel. (After Merculiano.)

FAMILY 1. SEPIIDAE, d'Orbigny. Body wide and flattened ; fins narrow and extending the whole length of the body (Fig. 298^{bis}). Shell calcareous and laminated, forming the "sepion." Genera—*Belosepia*, Voltz ; a rudiment of the rostrum and phragmocone present ; Eocene. *Sepia*, Linnaeus ; shell with a rostrum (Figs. 262, B, and 299) ; British. *Sepiella*, Steenstrup ; shell without a rostrum. FAMILY 2. SEPIOLIDAE, Leach. Body short, rounded at the aboral end ; fins rounded, inserted on the middle of the length of the body. Shell chitinous, narrow and shorter than the body, or absent. Genera—*Sepiola*, Leach ; head united to the mantle in the anterior (dorsal) region ; a fossorial British genus. *Rossia*, Gray ; head not united to the mantle ; British.

Stoloteuthis, Verrill, and *Inioteuthis*, Verrill, have no internal shell. *Heteroteuthis*, Gray. *Euprymna*, Steenstrup. FAMILY 3. IDIOSEPIIDAE. Steenstrup. Body elongated, with rudimentary terminal fins. Internal shell almost lost. Genus—*Idiosepius*, Steenstrup ; this tiny Cephalopod is only 1½ centimetre long, and has a mucous pore at the aboral extremity of the body ; it inhabits the Indian Ocean. FAMILY 4. SEPIADARIIDAE, Steenstrup. Body short ; the mantle fused to the head anteriorly (dorsally). No shell. Genera—*Sepiadarium*, Steenstrup ; fins short, situated at the aboral extremity of the body ; from the Pacific Ocean. *Sepioloidea*, d'Orbigny ; fins nearly as long as the body ; Australian. FAMILY 5. LOLIGINIDAE, Leach. Body elongated and conical ; fins triangular or

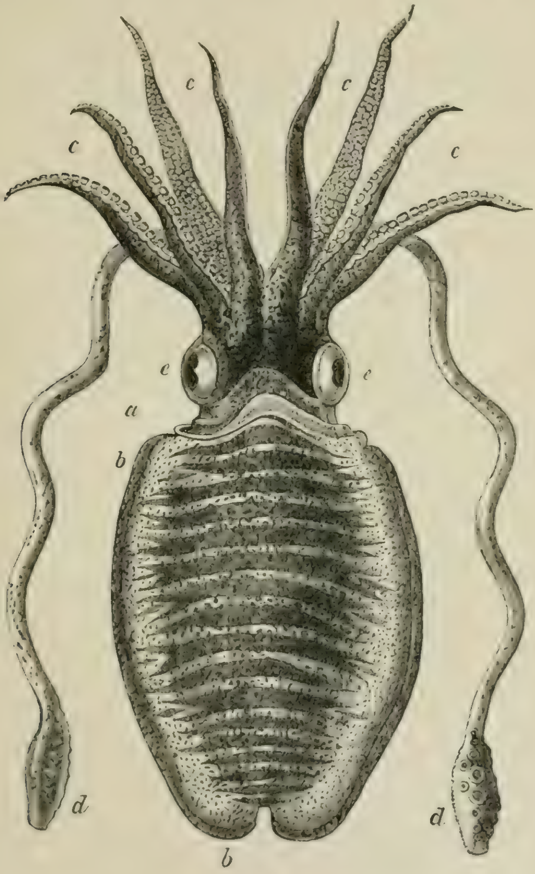

FIG. 299.

Sepia officinalis, dorsal view of a dead specimen, with the short arms spread out and the long arms pulled out of their sacs. *a*, neck ; *b*, lateral fins ; *c*, the eight shorter arms ; *d*, the two long tentacular arms ; *e*, the eyes. (From Lankester, after Owen.)

rounded, and extending farther forward than the aboral half of the body. Tentacular arms partly retractile. The shell is a well-developed chitinous gladius (Fig. 263). Genera—*Loligo*, Lamarck; fins triangular, confined to the aboral half of the body; British. *Sepioteuthis*, de Blainville; fins prominent but rounded, extending over the whole length of the body. *Loliolus*, Steenstrup. *Loliguncula*, Steenstrup. The following fossil genera, known by their gladius and ink-sac, have been placed near *Loligo*:—*Teuthopsis*, Deslongchamps. *Beloteuthis*, Münster, and *Geoteuthis*, from the Lias, and *Phylloteuthis*, Meek and Hayden, from the Cretaceous, are distinguished by their broader gladius. *Plesioteuthis*, Wagner, from the Jurassic and Cretaceous, has a long and narrow gladius.

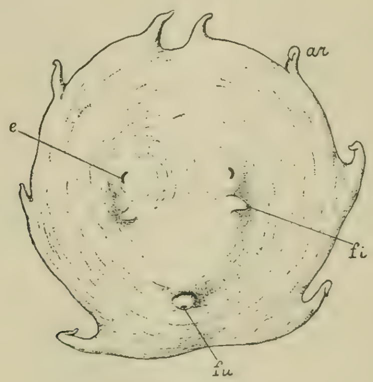

FIG. 300.

Opisthoteuthis depressa, Ijima and Ikeda, dorsal aspect. *ar*, arms; *e*, eye; *fi*, fin; *fu*, funnel. (After Ijima and Ikeda.)

SUB-ORDER 2. OCTOPODA.

These Dibranchia have only eight arms, which are all similar and are longer than the body. The body is short and rounded aborally. The suckers are sessile. The heart is not contained in the coelom. There are no nidamentary glands. The Octopoda comprise two tribes, the Leioglossa and Trachyglossa.

TRIBE 1. LEIOGLOSSA.

The members of this tribe have no radula. All the arms are united together by a complete membrane. Fins are developed on the sides of the body.

Family CIRRHOTEUTHIDAE, Keferstein. Arms united by a membrane, and bearing tentacular filaments on either side of the suckers (Fig. 260). Genera—*Cirrhoteuthis*, Eschricht; the pallial sac prominent and the fins large; a pelagic form. *Opisthoteuthis*, Verrill; body flattened, with small fins; a deep-sea form (Fig. 300). *Vampyroteuthis*, Chun; four fins. Some fossil Octopoda bearing fins are known; *e.g.* *Palaeoctopus*, Woodward, from the Cretaceous.

TRIBE 2. TRACHYGLOSSA.

These are Octopoda with a radula and without true fins.

FAMILY 1. AMPHITRETIDAE, Hoyle. The funnel is attached to the middle line of the mantle, dividing the pallial aperture into two. The eight arms are united by a membrane. Genus—*Amphitretus*, Hoyle; pelagic. FAMILY 2. ALLOPOSIDAE, Verrill. All the arms united by a membrane. The mantle is joined to the head by a dorsal band and two lateral commissures. Genus—*Alloposus*, Verrill; pelagic. FAMILY 3. OCTOPODIDAE, d'Orbigny. Arms long and equal, without a true interbrachial membrane. The hectocotylus is not caducous. No cephalic aquiferous pores. Genera—*Octopus*, Lamarck; the suckers in two rows on each arm; British. *Eledone*, Leach; a single row of suckers on each arm; British. *Scaeurgus*, Troschel. *Pinnoctopus*, d'Orbigny. *Cistopus*, Gray. *Japetella*, Hoyle. FAMILY 4. PHILONEXIDAE, d'Orbigny. Males and females naked. The hectocotylus is autotomous. The arms are unequal in size but similar in the two sexes. Aquiferous pores are present on the head and funnel. Genera—*Tremoctopus*, Delle Chiaje; the two dorsal pair of arms are united by a membrane. *Ocythoë*, Rafinesque; without an interbrachial membrane (Fig. 287). FAMILY 5. ARGONAUTIDAE, Cantraine. The hectocotylised arm autotomous. The extremities of the dorsal arms are enlarged in the female (Fig. 301), and secrete a shell in which the body is contained. The males are very small and naked. Genus—*Argonauta*, Linnaeus.

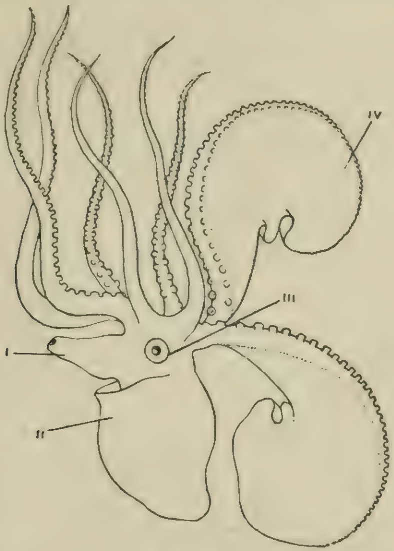

FIG. 301.

Argonauta argo, Linnaeus, left side of the female. I, funnel; II, mantle; III, eye; IV, dorsal webbed arm. (After Verany.)

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